

TOWARDS A CONSTRUCTIONAL MORPHOLOGY OF CICHLID FISHES (TELEOSTEI, PERCIFORMES)

by

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SUMMARY

Based on *ca* 100 lacustrine cichlid species and following a holistic procedure of functional morphology, this paper analyses what constraints spatial relations of structures may set on the compatibility of functions. Among the many feeding behaviours of cichlids two groups are distinguished: (1) those in which powerful biting with the oral jaws are involved and (2) those in which the food is directly sucked into the buccal cavity without prior manipulation by the oral jaws. Related to the core functions "biting" and "sucking only" two types of oral jaw apparatuses (OJA) are distinguished and compared (*i.e.* comparison in a functional context). Taking the head as the available space (constructional component) it is subsequently investigated what spatial demands there are to accommodate these two types of OJA together with other apparatuses (comparisons in a constructional context), and how these spatial demands 'affect' the function of the other apparatuses, especially the expansion apparatus (EA) and outer head shape (OHS, part of the locomotory apparatus). It is demonstrated that the suction feeding and biting can be combined to a certain extent and at certain costs. Increase in streamline is inversely related to active head expansion, and in biters is also inversely related to the size of the maximally expanded buccal cavity. The possible implication for the tripartite compatibility of (1) the various types of locomotion, (2) suction feeding and (3) feeding involving oral manipulation of the food, are discussed.

For a number of other apparatuses (*e.g.* gill-apparatus and pharyngeal jaw apparatus) similar but less extensive analyses of spatial relations are made. Among these, examples are given of diversity in spatial relations: *e.g.* the relations between a particular outer head shape and differing head structures (see the section on 'inner ear').

The complex and indirect relations between the food-category eaten and the structure of the feeding apparatus are discussed.

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INTRODUCTION

Among vertebrates, the cichlid fishes of the Great Lakes of Africa present a unique reservoir of numerous morphologically similar organisms of unrivalled ecological diversity. Such a reservoir is ideal for comparative functional morphology. However, in comparison with the many studies on the systematics, phylogenetic relationships and ecology, relatively few publications deal with the functional morphology of these fishes. LIEM (1974) at Harvard University was the first to explore this field and important papers on function and morphology of cichlids are still being published by him and his students (*e.g.* LIEM & KAUFMAN, *in press*). So far Liem has focussed on the experimental analysis of the feeding repertoires, their evolutionary significance and their underlying morphology. The main interest of the cichlid research group at Leiden University concerns constructional and ecological morphology, *i.e.* the relation of integrated form-function complexes with ecology. It is a long way from anatomy to ecology, but by starting from both ends with well attuned programmes we are optimistic about the eventual multidisciplinary results. Among the studies in the 'ecological track' of our research (*e.g.* VAN OIJEN *et al.*, 1981; WITTE, 1981, *in press*; VAN OIJEN, 1982; HOOGERHOUD *et al.*, 1983), the work of HOOGERHOUD (*in prep.*) on the intratrophic ecological and morphological differentiation of the molluscivores has come closest to morphology. In the 'morphological track' of our research (*e.g.* BAREL *et al.*, 1974; ANKER, 1978; HOOGERHOUD & BAREL, 1978; GALIS & BAREL, 1980; OTTEN, 1983) the present paper is, as yet, the nearest step towards ecology. The paper deals mainly with the analysis of spatial relations between apparatuses performing different functions. Based on *ca* 100 cichlid species from various African lakes and following a holistic procedure of functional morphology, I have attempted to analyse whether spatial relations may set constraints on the

compatibility of functions. Insight into the compatibility of functions is ecologically relevant because it provides insight into the ecological potentials (*potential* niche width) of a species.

METHODS

The Holistic Procedure of Functional Morphology

The holistic procedure of functional morphology (analysing what an integrated whole of forms and functions means) involves at least four steps:

(1) *The critical assessment of functions and of form-features*

Form assessment is hardly considered in this paper. The presence of, for instance, a lower jaw, suspensorium and adductor muscle in the oral jaw apparatus (OJA) is taken as a starting point and only for the qualitative and quantitative differences in shape and size is an explanation sought.

Concerning the determination of function, two examples are given. The first is the determination of a *core function*: a function common to a set of more complex functions considered in a certain context (p. 361). The second example concerns the transition series: food-feeding-function (p. 404).

(2) *The form-function and form-form relations within a functional component*

For every function it is to be investigated what the constituent form-features are, and what the relations between these features and the function are (comparative method) or better how the form-features should be when only the functional demand is taken into account (deductive method). The function plus its constituent form-features is called a *functional component* (FC) (VAN DER KLAUW, 1945; DULLEMEIJER & BAREL, 1977). The relations between function and form should ideally be expressed in a mathematical formula (DULLEMEIJER, 1958; DULLEMEIJER & BAREL, 1977): $F = f(a, b, c, \dots)$, where F is the biological function, f a mathematical formula of which the form-features $a, b, c \dots$ are the parameters.

Taking the form-features in such a formula as variables it can be calculated in which range of forms a certain function can be performed (deductive method, DULLEMEIJER, 1958, 1974). More often than not such ranges are extensive. However, the number of solutions may be decreased when further demands are introduced (*e.g.* minimal energy costs). Even after such optimization one is often left with a range of morphological solutions from which no further selection can be made without introducing extrinsic criteria: *e.g.* limiting demands from form-features of other functional components (and thus - indirectly -

from other functions, see step 3). In this paper the functional component for the static biting force of the lower jaw is taken as an example of form-function and form-form relations within an FC.

(3) *The spatial (= geometric) relations between form-features*

By analogy with the functional component, the *constructional component* is distinguished, which describes the geometric relations of form-features belonging to one or more functional components within a defined space. As with the functional component, these spatial relations are ideally given in a mathematical formula and deductive procedures should be applied: with various form-features as variables it should be computed what constellation of the constructional component can accommodate a required form. To date mathematical formulations of constructional components are not available and even consistent qualitative descriptions of topographical relations of functionally relevant form-features within a defined space are rare. In this paper mainly *qualitative* differences in the spatial relations between form-features of the following apparatuses* are considered: expansion apparatus (EA) \times oral jaw apparatus (OJA); OJA \times outer head shape (OHS, part of the locomotion apparatus), OHS \times EA, OHS \times inner ear, OJA \times EA \times gill apparatus (GA), pharyngeal jaw apparatus (PJA) \times EA; and OHS \times EA \times OJA \times GA \times eye shape.

(4) *Constructional morphology: the integration of functional components*

This is an essential step in holistic studies of functional morphology (DULLEMEIJER, 1974; ZWEERS, 1979). Functional morphology dealing with the mutual dependence of functional components (FC's) (*i.e.*, with the constraints on the integration) is called constructional morphology (DULLEMEIJER & BAREL, 1977). Theoretically the integration of FC's requires the study of two classes of relations: between the functions and between the form-features of the different components (fig. 1). The direct relation between various functions is by tradition the province of physiology; in functional morphology these relations are only indirectly studied via the form-relations (fig. 1). The relations between form-features of different FC's concern their spatial relations (see above). Both spatial demands *and* functional demands determine what range of certain form-features is allowed. The presence or absence of an overlap between the ranges of form-features for different functional components determines whether functions are deductively compatible. Examples of the morphological constraints upon function compatibility are given.

* For the subtle differences between our use of the term *apparatus* and *functional component* see DULLEMEIJER & BAREL, 1977.

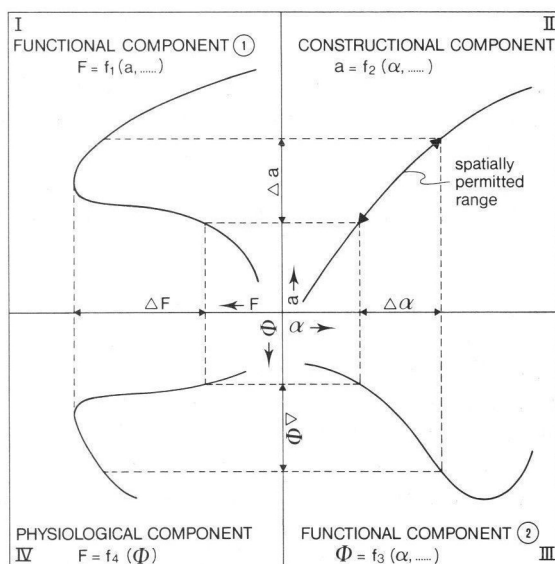


Fig. 1. The elements of constructional morphology and their interrelations. In a functional component, the relation between a biological function (F , Φ) and its constituent form-features (*e.g.* a and α) are analysed. In a constructional component the geometric relations between form-features (a , α) of different functional components are studied. The physiological component gives the relations between functions (F , Φ). In constructional morphology, the physiological component is derived from the relations between the functional and constructional components. Ideally all relations should be given as mathematical formula (f_1 , f_2 , f_3 , f_4). The figure further illustrates how one constraint (*e.g.* α constructionally limited to $\Delta\alpha$) determines what ranges of functions and function combinations can be realized. Note for instance that if only $\Delta\alpha$ is allowed, the optimum of function Φ is excluded.

MATERIAL AND TECHNIQUES

Reference measure: Unless stated otherwise all comparisons are made with the neurocranial length (NL, defined in HOOGERHOUD & WITTE, 1981) as a reference measure: *e.g.* "the adductors of biters are wider than those of suckers" should be read as "for specimens of the same NL, the adductors of biters are wider than those of suckers".
Abbreviations: Species names are followed by two capitals indicating the lake of origin. These abbreviations plus those of the various apparatuses are given in the Appendix.
Materials: The specimens studied plus their basic data (*e.g.* lower jaw length and/or neurocranial length, symbols used in graphs) are given in table I in the Appendix.

RESULTS

Oral Jaw Apparatus (OJA): Form-Function Relations

Core functions

Feeding in cichlids may involve five actions on the food: (1) manipulation by the oral jaws, (2) transport into and (3) through the buccal

cavity, (4) reduction by the pharyngeal jaws and (5) transport into the esophagus. Even when completely different food categories are involved the functional demands within one act often do not differ completely. Jerking algae from rocks, scraping scales from fishes or wrenching snails from their shells involve different and highly complicated manipulations of the food-item by the oral jaws. However, the three feeding types share the functional demand of a forceful bite. Such a shared part-function will be called a *core function*.

Not all five steps which feeding of cichlids may potentially comprise (see above), must be involved. Zooplankton in the stomach is often intact and thus not trituated by the pharyngeal and oral jaws. Manipulation by the oJA which is observed in *e.g.* lepidophages, algae scrapers and insect-pickers, does not occur in the feeding-acts of zooplanktivores, phytoplanktivores and many piscivores. Food uptake into the buccal cavity in the latter trophic categories is direct, *i.e.* as part of the water entering the mouth (suction feeding or straining) whereas this uptake is indirect when oral manipulation is involved. The morphological requirements of the oJA (comprising suspensorium, oral jaws and m. adductor mandibulae, mAM) are likely to be different for direct and indirect food uptake and raise the question whether, or to what degree, the two ways of feeding can be combined; *viz.* what morphological constraints are there on combining a manipulation type of feeding with *e.g.* suction feeding. Can the morphological requirements for oral manipulation be superimposed on the morphological requirements for suction feeding or do they interfere? This problem is not only important for constructional morphology but also for ecology. If oral manipulation could be simply added to suction feeding, then the 'manipulators' would seemingly be trophically more versatile than the obligate suction-feeders. As I shall demonstrate there are morphological constraints in combining suction feeding with manipulation: the manipulation type of oJA 'influences' the expansion apparatus (EA). Moreover, as will be illustrated in this paper, there are complex spatial relations between the oJA, EA, locomotion apparatus, gill apparatus and eye-shape. After we have studied (1) these spatial relations, (2) the resulting constraints on function combinations and (3) the ecological significance of these constraints, we would be able to discuss the morphological basis of ecological versatility. That ultimate goal of ecological morphology is not yet reached, but hopefully this paper provides a first step, a few examples and a method.

The biting and sucking type of oJA

As mentioned above a strong biting force is a common demand (core

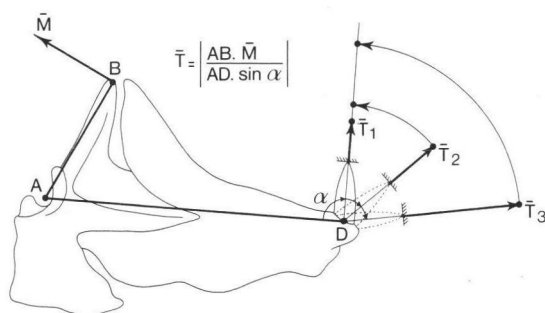


Fig. 2a. Model for the static biting force (\bar{T}) of a rostral tooth of the lower jaw resulting from contraction (\bar{M}) of the A_2 -part of the m. adductor mandibulae. The working line of the muscle is estimated to be approximately perpendicular to the primordial process (AB). The effect of increasing tooth-inclination (increasing α) on \bar{T} is illustrated by \bar{T}_1 , \bar{T}_2 and \bar{T}_3 of which the scalar values can be compared on the working line of \bar{T}_1 .

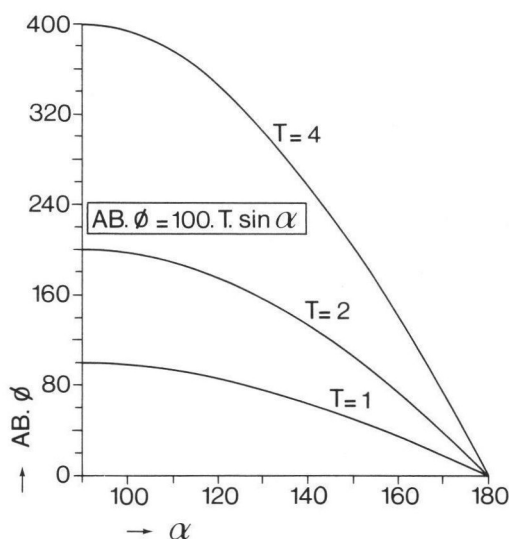


Fig. 2b. Illustration of form-relations (*i.e.* size AB, \emptyset against position α) within a functional component, *viz.* the model and formula of the static biting force presented in fig. 2a. As only a qualitative insight in the effect of increased biting force on the form-relations was required, the scalar unit of the contraction force per unit of area was arbitrarily set at 1 which makes $M = \emptyset$ (\emptyset : cross-section of A_2 part of the adductor mandibulae muscle) and the lower jaw length (AD) was standardized arbitrarily at 100. The figure demonstrates that with increase in biting force (\bar{T}) tooth-inclination (α) (*i.e.* position-change) becomes increasingly effective in decreasing the contribution from the size parameters (AB, \emptyset).

SUCKERS

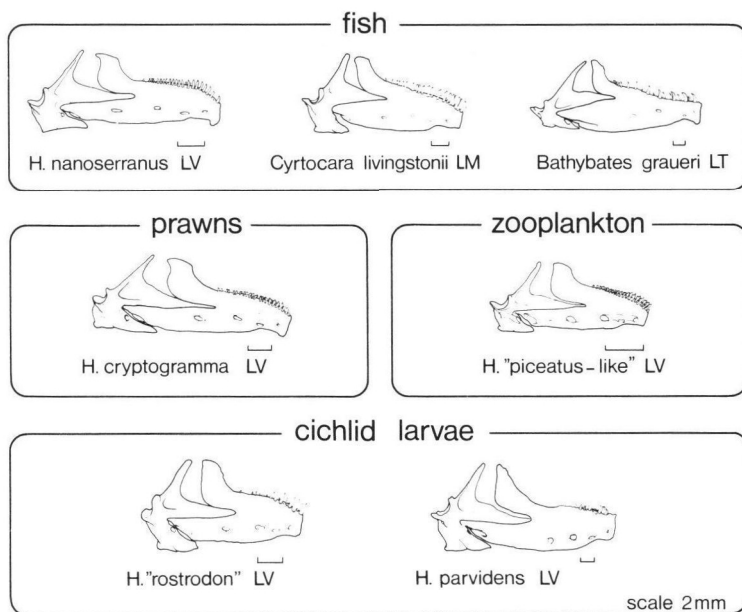


Fig. 3. A sample of the lower jaws from the biting and from the sucking type of oral jaw apparatus (OJA). (Lower jaws drawn by W. Wilhelm.).

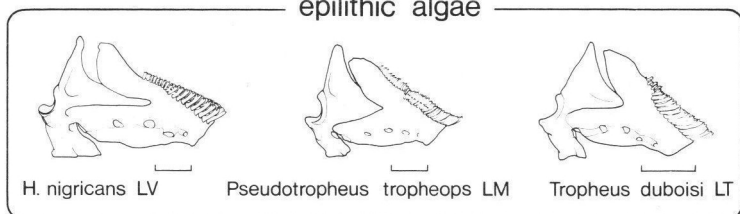
function) of many (but not all)* feeding types involving oral manipulation of the food. Cichlids with a feeding type involving powerful biting will be called '*biters*' in this paper, whereas those in which food is only sucked directly into the mouth will be classified as '*suckers*'. In this first approach to the question of morphological constraints on the combination of a manipulation type of feeding with suction feeding, only the core functions "*suction feeding*" and "*forceful biting*" are considered. As explained above, this does not mean that complex feeding acts like scale scraping and oral shelling of molluscs can be reduced to forceful biting only. The two feeding acts differ in many aspects, but the morphological requirements resulting from these *differing* functional demands are not investigated in this initial study.

The following procedure, involving the form-function-relation of the OJA, were used to group biters and suckers:

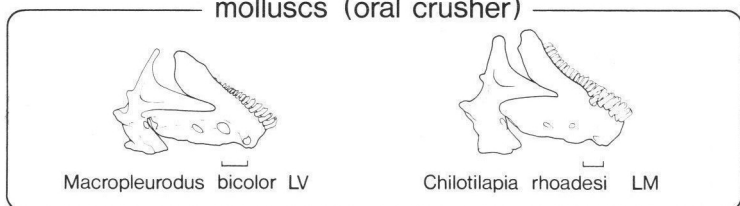
* Scraping epiphytic diatoms requires a delicate manipulation with little force from the oral jaws.

BITERS

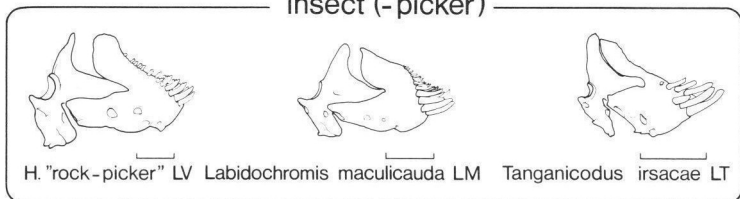
epilithic algae



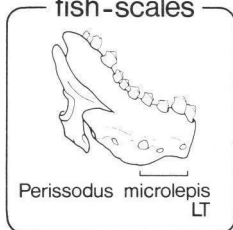
molluscs (oral crusher)



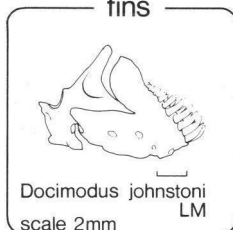
insect (-picker)



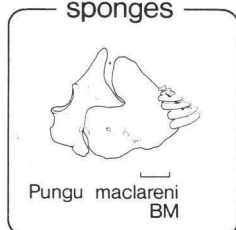
fish-scales



fins



sponges



1) The oja's of biters of which the actual feeding behaviour is known (epilithic algae scrapers and oral shelling molluscivores) were compared with those of suckers of which the actual feeding behaviour is known (piscivores and zooplanktivores). The following functionally understandable differences were observed: In epilithic algae scrapers and oral shelling molluscivores both the lower jaw and suspensorium are reinforced, thicker elements and the suspensorium-neurocranium articulations are strengthened. From the formula for the static biting force of the lower jaw (fig. 2a) it is evident that for each lower jaw

length (AD) an increase in the muscle force (\bar{M}), in the length of the primordial process (AB), and in the tooth-inclination (α), all contribute to an increased biting force. Usually all three, but at least two of these increases are observed in the oJA of biters. Taking AD as horizontal, the teeth and their dentigerous area have a significantly more (rostrad) inclination in biters (fig. 3). For each lower jaw length (AD), the primordial process (AB) of biters is often longer than, or at least within the range of, the suckers (fig. 4). For each lower jaw length there is a significant difference in the mAM cross-section (and thus most probably in the muscle force): not only do biters have greater depth and width of the mAM (fig. 6), the cross-sectional shape is also nearly square whereas it is more triangular in suckers.

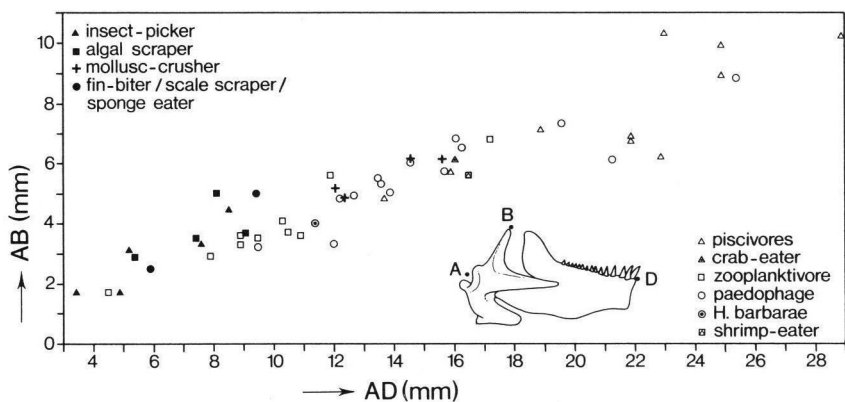


Fig. 4. The relation between the length of the primordial process (AB) of biters and suckers with the lower jaw length (AD) as a reference measure. Each point represents a different species. The species are from various lakes (see table I). Open symbols are suckers, solid symbols and + are biters.

2) For species of which the feeding behaviour has not been observed and with oJA's resembling those of suckers or biters described above, the stomach contents should not suggest a feeding behaviour excluded by the structure of their oJA's. The oJA's of feeders on prawns (the "tridens"-group of GREENWOOD, 1974 and GREENWOOD & BAREL, 1978) strongly resemble those of (other) suckers. It is not unlikely that the elusive and translucent prawns *Caridina* (VAN OIJEN, *pers. comm.*) are sucked in by an oJA and expansion apparatus which are both similar to that of piscivores.

The oJA's of paedophages can be classified with the suckers. Although the lower jaws, suspensoria and other head features of some

paedophages are at the higher extreme end of the range of suckers, they are still separated from the range observed for the biters. Paedophages with such reinforced lower jaws include and resemble the species for which WILHELM (1980) observed snout-engulfing during which the paedophage extracted the eggs from the mouth of a brooding female. Eggs spat out by the female were sucked from the water column by this paedophage. Snout-engulfing is a manipulation act of the oral jaw apparently requiring some reinforcement of the oJA. However, if egg-extraction from the brooding female is mainly caused by powerful sucking, then the grasp on the head of the female is mainly due to underpressure and not so much to contraction of the mAM which, in cross-section, does not differ trenchantly from that of other suckers (fig. 6).

The lepidophages from Lake Tanganyika, fin-eater, sponge-eater and insect pickers fit within the group of other biters. Their (presumed) feeding acts are likely to involve forceful biting.

In summary: the main result of the foregoing analysis is a consistent distinction between biters and suckers based on morphological differences in their oJA. This classification, based on functional morphology, is independent of the lakes of origin of the fishes.

The biters comprise epilithic algae scrapers, oral shelling molluscivores, scale scrapers, a fin biter, a sponge eater and insect pickers. The suckers cover piscivores, zooplanktivores, prawn eaters and snout-engulfing paedophages.

oJA: constructional and functional context

So far the form-function relations of the oJA were studied in a *functional context* only, *i.e.* from isolated oJA's. The kind of fish built around these apparatuses -so to speak- was not considered. In the *constructional context* the oJA is 'reintegrated' in the fish: *i.e.* part of a certain space (constructional component) in which other apparatuses are also accommodated. This could imply a spatial interdependence between form features belonging to different apparatuses. Whether as a result of these spatial relations the functions are also affected remains to be investigated. In this paper the head is chosen as the available space, *i.e.* as the constructional component. The spatial relations of the form-features investigated concern mainly size parameters (and not angular measurements only) and therefore a reference measure is needed. The neurocranial length (NL) is selected which, as an undeformable element spanning the whole length of the head, seems a good indicator of the head size. Head-volume would have been a better indicator, but, for technical reasons, this measure could not be taken (*e.g.* many

specimens were partly dissected; undissected heads were in different expansion positions).

In the constructional context it appears that biters often have a relatively shorter lower jaw or at least a jaw length within the range of that of the suckers (fig. 5) with the same NL.

With regard to NL the primordial processes (fig. 2a: AB) of biters are as long as or even shorter than those of suckers.

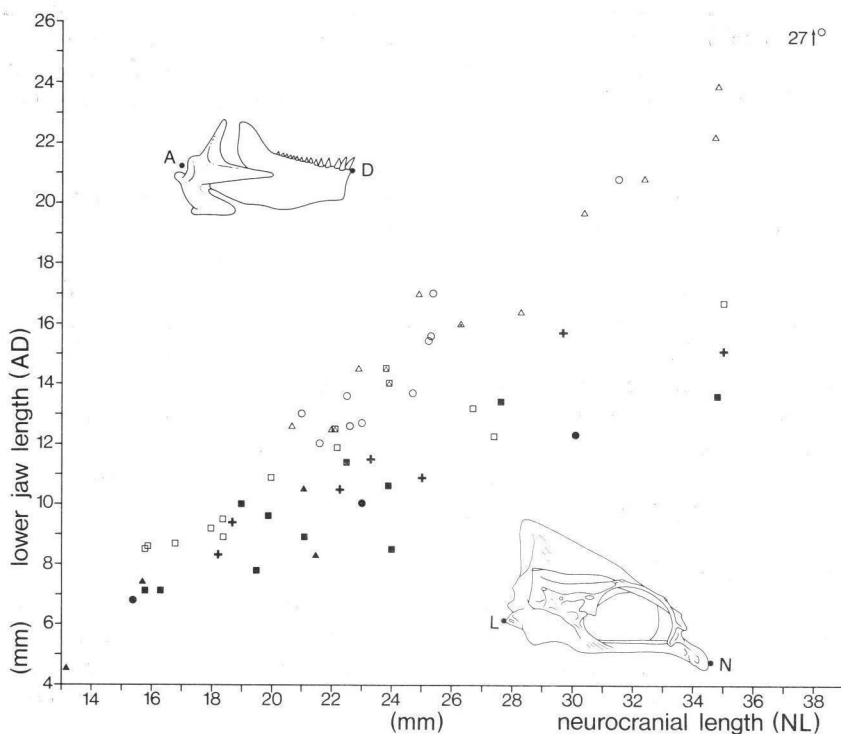


Fig. 5. The relation between lower jaw lengths (AD) of biters and suckers with the neurocranial length (NL) as a reference measure. Symbols and conditions as in fig. 4.

Whereas in the *functional* context the mAM width and depth of biters and suckers were significantly different, this separation is less evident in the *constructional* context (compare figs. 6 and 7). In the latter context there is an increased overlap in the ranges of the muscle-depth between biters and suckers. However, in the constructional context too the muscle-widths and often the depths as well, are larger in the biters and thus need more space.

From the foregoing it is evident that, in contrast to the functional context, from a comparison of the oJA-parameters in the constructional context no unequivocal evidence for differences in the static biting force in the latter context can be derived. As an indicator of the overall effect of the morphological differences on the biting function an index of static biting force (b) was calculated and plotted against NL (and lower jaw length, AD). The formula of the index reads:

$$b = (AB \cdot A_2d \cdot A_w) / (2 \cdot AD \cdot \sin \alpha)$$

(A_2d = depth of the A_2 part of mAM, A_w the width of the mAM, AB the length of the primordial process and α the tooth inclination, cf. figs. 2a, 7). When \bar{F} is the unitvector of muscle-force per mm^2 , then $b\bar{F}$ is an estimate for the static biting force (\bar{T} in fig. 2a) resulting from contraction of the A_2 (the main operator of the lower jaw). The cross-section of A_2 in biters is more a square whereas it is a triangle in suckers. As the formula is based on a triangle, the b calculated for biters is an underestimate of their real b 's. However, this underestimation makes the conclusion only conservative. From figs. 8 and 9 (and with the foregoing in mind) it can be seen that both in the constructional and functional context there is a striking difference between the indices of static biting force of biters and suckers.

The procedure followed would be unwantedly cumbersome were the differences in biting force the only aim. A direct calculation of b , without first investigating the correlation between each oJA-parameters and NL, would have been more efficient. However, information about these correlations is needed when the "spatial costs" of accommodating the two types of oJA are to be considered. The spatial requirements of the biting and sucking types of oJA (see above and figs. 4, 6) are mainly taken for granted, *i.e.* there is as yet no full (but see below) deductive proof that these requirements are an optimal solution. The methods and techniques of OTTEN (1983) could be instrumental to such proofs. For a different model (biting *with* protrusion) he calculated what points in the oJA of the insectivorous *Haplochromis elegans* LG (not a biter) required minimal positional change to improve the biting-force. The oJA thus calculated was in good agreement with the oJA of the biter (epilithic algae scraper) *H. nigricans* LV.

In fig. 1b the relations between the size-parameters (primordial process length AB and muscle cross-section Φ) and position parameter (inclination of the teeth α) of the oJA are given for various biting forces. The figure demonstrates that with increasing biting-force, increase in tooth-inclination becomes progressively more effective in reducing the contribution of the size parameters (and thus of space requirements). In this light and within the limits of this admittedly approximative model for the biting force, the marked inclination of the dentigerous

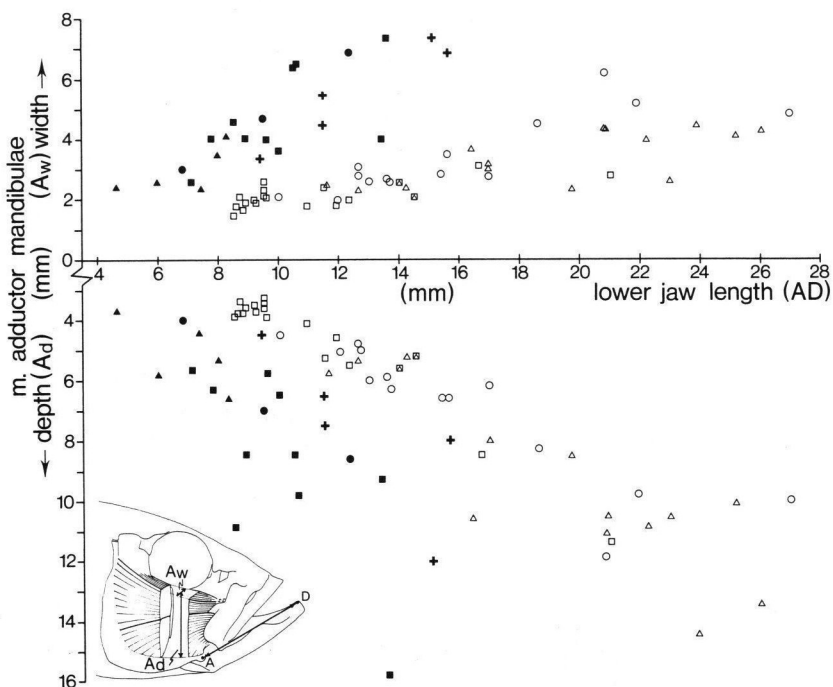


Fig. 6. The relation between the widths (A_w) and the depths (A_d) of the m. adductor mandibulae of biters and suckers with the lower jaw length (AD) as a reference measure. Symbols and conditions as in fig. 4.

areas of the lower jaw of biters could be interpreted as a (material and) space-saving solution selected for this reason from the various morphological options available to increase the biting force of the oja. The space-requirements for an equal biting force are progressively less with increasing inclination (fig. 2b).

Oral Jaw Apparatus (OJA) and Expansion Apparatus (EA)

Introduction

The expansion apparatus is part of the feeding apparatus to which the oja also belongs. Biting a prey or sucking it directly into the mouth could be looked upon as two, anatomically conflicting ways of getting food into the buccal cavity. As this combination concerns alternatives for the same functional demand (obtaining food) but involves different food categories, the functional balance between the oja and the ea is an indication of the degree of polytrophic capacities of the feeding ap-

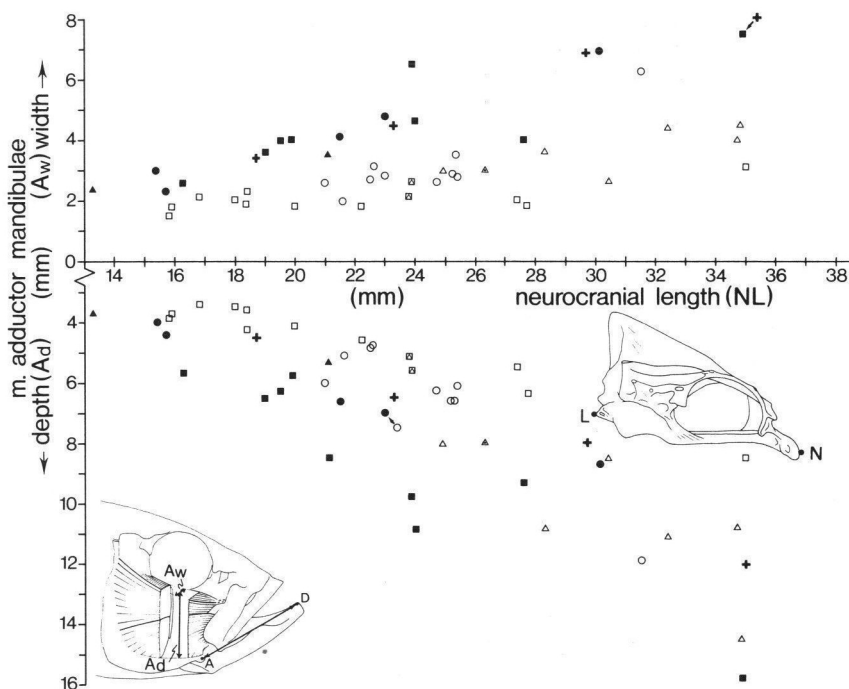


Fig. 7. The relation between the widths (A_w) and the depths (A_d) of the m. adductor mandibulae of biters and suckers with the neurocranial length (NL) as a reference measure. Symbols and conditions as in fig. 4.

paratus and as such highly relevant for a morphologically based prediction of the ecological capacities of a species.

Expansion apparatus: form-function and spatial relations

The functional relations (*i.e.* kinetics) within the EA have been investigated by me and will be published elsewhere. A short summary, from which the impact of form-change on function can be derived, is given here. Fishes for which suction feeding has been experimentally investigated, have expanding oro-branchial cavities shaped as cylinders or truncated cones (MULLER & OSSE, 1983). Most casts of cavities made from a maximally expanded head in cichlids from Lake Victoria are indeed reasonably cylindrical or conical. At the level of the hyoid-suspensorium articulation, the maximum radius (C_{max}) of the cross-section of the "pharyngeal circle" (fig. 10) of a cylindrically shaped cavity can be calculated from two anatomical parameters: the

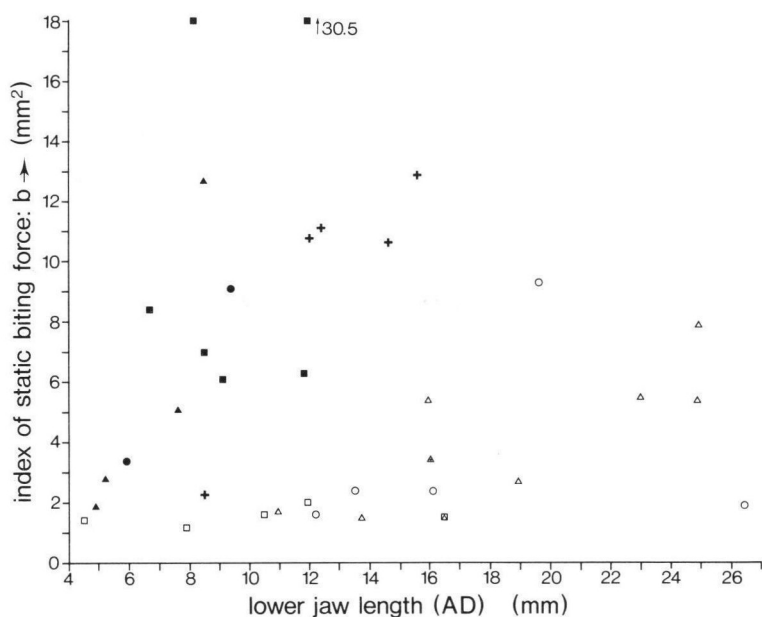


Fig. 8. The relations between the indices of static biting force (b, explained in the text) of biters and suckers with the lower jaw length (AD) as a reference measure. Symbols and conditions as in fig. 4.

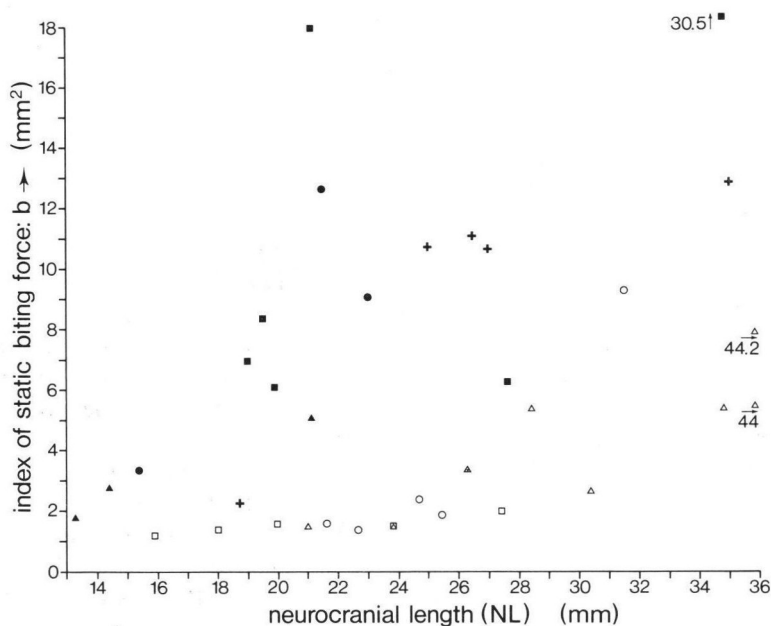


Fig. 9. The relations between the indices of static biting force (b, explained in the text) of biters and suckers with the neurocranial length (NL) as a reference measure. Symbols and conditions as in fig. 4.

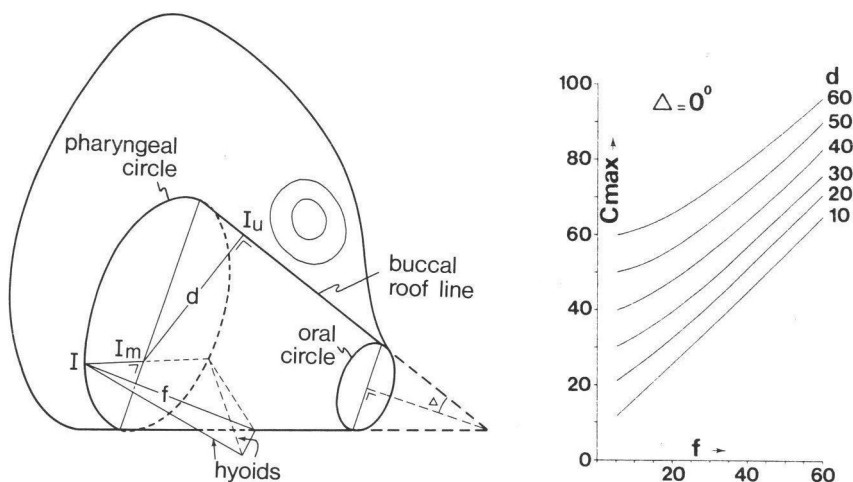


Fig. 10. Model for the conically shaped expanded buccal cavity. I: articulation point of hyoid with suspensorium. (Adapted from Barel, *in prep.*).

Fig. 11. The relations between the maximum radius (C_{\max}) of the pharyngeal circle (of a cylindrical buccal cavity: $\Delta = 0^\circ$) and the length of the hyoid (f) and sagittal distance (d) of the hyoid-suspensorium articulation to the buccal roof (see fig. 10). (From Barel, *in prep.*).

hyoid length (f) and the mid-sagittal distance of the hyoid-suspensorium articulation from the roof of the buccal cavity (d):

$$C_{\max} = d/2 + \sqrt{(d/2)^2 + f^2}$$

For cone shaped cavities the apical angle of the cone is to be included which makes the formula more complex but in the present context does not affect the conclusion drawn. The radii calculated from the formula are in accordance with those measured directly from the casts. From the graphs in fig. 11, based on the formula above (and from the formula itself) it is evident that decreasing f and/or d decreases C_{\max} . For the following topographical reasons an effect of OJA -differences on f and d could be expected:

1) Measured in a head-bound reference frame, hyoid movements are the main kinematic input of head-expansion during feeding (BAREL, *in prep.*). In time, generally the first task of hyoid movements is the rapid opening of the jaws. To fulfill that task the hyoid should be on the medial face of the suspensorium, *viz.* there should be no space between the medial side of the suspensorium and the lateral side of the greater, caudal section of the hyoid (BAREL, *in prep.*). A further requirement for effective expansion is a very small initial size of the mouth-cavity.

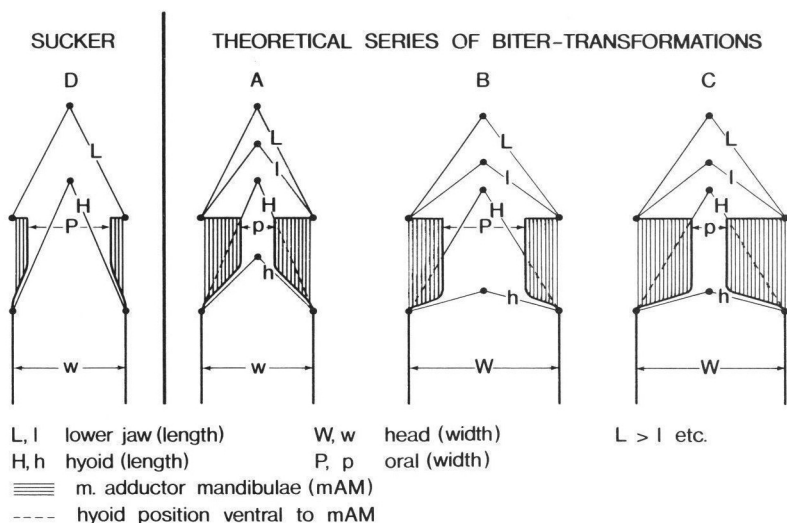


Fig. 12. Theoretical series of effects of "accommodating the broader mAM of biters" on the position of the hyoid and on the angle between the hyoid rami and between the lower jaw rami. The figures represent highly schematic dorsal views on the considered head structures. Hyoids and lower jaws of biters may be shorter than those of suckers. The parameter combinations most observed in biters are: W, p, H, l or L; *i.e.* the accommodation of a broader mAM of biters results in a wider head, a wider angle between the hyoid rami and between the lower jaw rami and (see fig. 15) in a ventrad shift of the hyoid symphysis.

Therefore the hyoid should be elevated to such an extent that its symphysis reaches the buccal roof. In this position the main part of the hyoid lies medial (and not ventro-medial) to the mAM.

The accommodation of a greater mAM-width found among biters has to be achieved through laterad and/or mediad extension of the muscle, which must effect the position and/or length of the hyoid (fig. 12). As the range of the hyoid lengths of virtually all biters is the same as that of suckers (fig. 13), and because the accommodation of the wider mAM is achieved through mediad (plus laterad) widening (fig. 12), the hyoids can no longer be accommodated entirely in the constricted space between the left and right mAM, and must take a lower position, as can be seen in fig. 15. After the foregoing statements, two questions remain: (1) why could not the head be broadened so that the hyoid could be accommodated medial to the muscle area of the suspensorium and (2) why should the hyoids of biters and suckers have approximately the same lengths? Neither of these questions can be satisfactorily answered as yet but are under investigation. Head width

is an important parameter of the head profile. The qualitative relation between head profile and locomotion is considered on p. 382 and will be quantitatively analysed by VAN LEEUWEN (*in prep.*). Head-widening would either increase the angle between the hyoid-rami or require longer hyoids. The preliminary results of my quantitative model for the expansion-apparatus indicate that neither of the two seems allowed (BAREL, *in prep.*).

The influence of the ventral shift of the hyoid symphysis on the *initial* volume of the buccal cavity remains to be investigated quantitatively, but I have the impression that the volume is larger in biters. A larger initial volume is unfavourable for suction. However, the shift is of advantage for the gill apparatus (p. 381) and the retained hyoid length (f) implies that, at least with respect to this parameter, there is no influence of the oJA on C_{max} .

2) The often strong decurvature of the ethmovomerine bloc in biters (fig. 33) is a requirement for an increased biting force (OTTEN, 1983). This decurvature (and probably other anatomical differences) lower the roof of the buccal cavity with respect to the parasphenoid. If the hyoid-suspensorium articulation would retain the same position, then d would diminish in biters and consequently so does C_{max} . However, with the orbital parasphenoid bar as a reference line, the ventrad shift of the buccal roof in biters is virtually always compensated for by a similar shift of the articulation (*cf.* figs. 13 and 14). Consequently there is, with the following exceptions, no difference in d between biters and suckers (fig. 13). Only in streamlined biters like *Perissodus paradoxus* LT does such a shift seem impossible as it would result in an unwanted increase in head depth.

As biters and suckers generally do not differ in the relative lengths of f and d , the pharyngeal circle of their fully expanded buccal cavities would have the same relative radius (C_{max}). This does not imply that the volume or shape of the cavities of biters and suckers are the same. For the following constructional reasons the oJA 's of biters have less voluminous buccal cavities which, in shape, are truncated cones or are rotationally asymmetric, while in suckers the cavities are larger and approximately cylindrical:

1) Related to their often shorter jaws and to their jaw shapes, the gape (oral circle: fig. 10) in biters is generally smaller than in suckers (fig. 16).

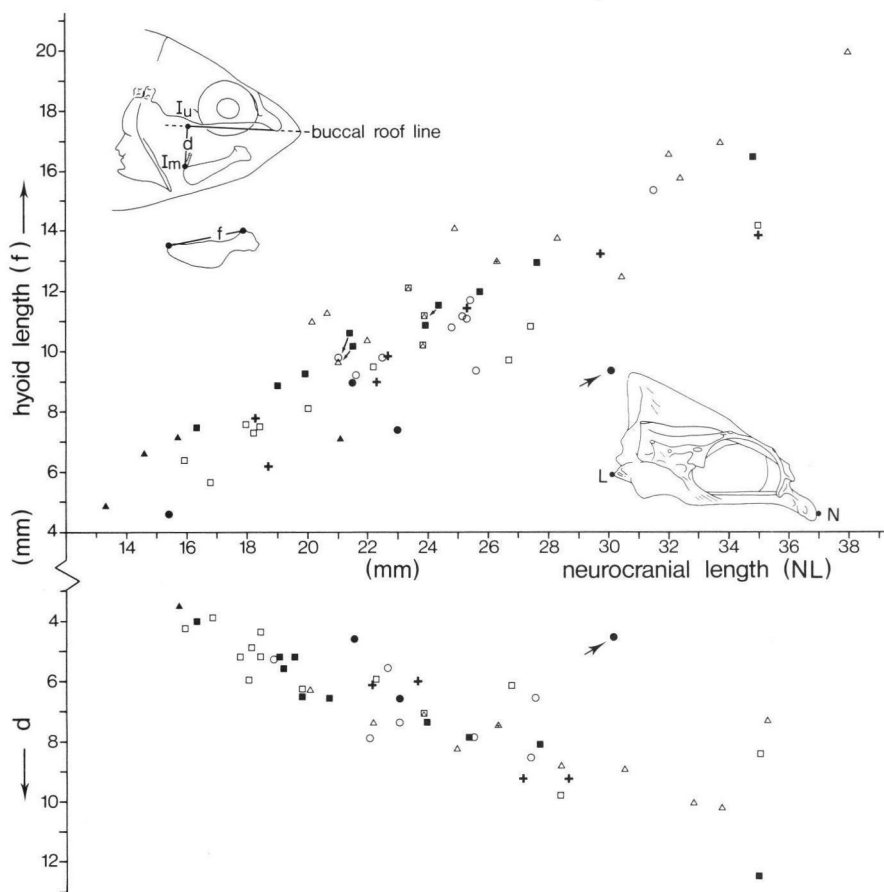


Fig. 13. Relation between biters and suckers for their lengths of the hyoids (f) and for their sagittal distances (d) of the hyoid-suspensorium articulation from the buccal roof. The neurocranial length (NL) is the reference measure. Larger arrows indicate f and d values for *Perissodus paradoxus* LT. Not of all specimens both f and d could be measured. Symbols and conditions as in fig. 4.

2) The smaller or virtually non-existent protrusion of biters makes their expanded buccal cavities shorter as compared with those of suckers with protrusion*. The reduced protrusion is related to the

* At least some fast swimming piscivores seem to have reduced protrusion. The functional significance is discussed on p. 403.

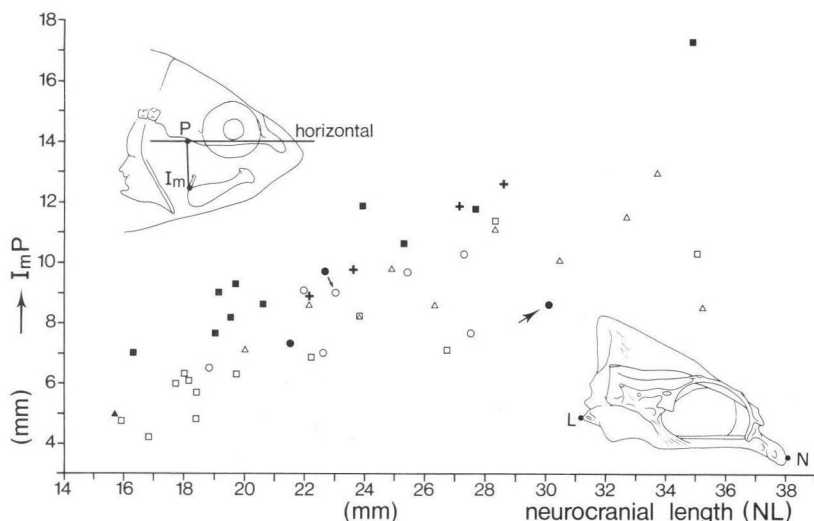


Fig. 14. Relations between biters and suckers for the sagittal distances (ImP) of the hyoid-suspensorium articulation to a horizontal line drawn through the parasphenoid. The neurocranial length (NL) is the reference measure. Large arrow indicates the ImP of *Perissodus paradoxus* LT.

shorter ascending process of the premaxilla of biters. This shortening is a requirement for an increased biting force of the oja (OTTEN, 1983).

3) The mediad expansion of the mAM constricts the buccal cavity and contributes to its cone shape (fig. 16F) or even affects the rotational symmetry (fig. 16H). In some biters, such as the oral shelling molluscivore *H. granti* LV, the gape is no longer circular, nor is it flat. There are indentations in the lateral profile (fig. 16G) which are hydrodynamically inefficient (MULLER & OSSE, 1983).

On morphological grounds a strongly diminished expansion capacity is expected for most scale-eating cichlids of Lake Tanganyika. Most have an extremely short hyoid (indicated in fig. 13), the mandibular symphysis is fixed, the adductor arcus palatini muscle is very short, and according to LIEM & STEWART (1976) the intermandibular muscle is absent.

Oral jaw apparatus and expansion apparatus: constructional morphology

From the foregoing it appears that a sucking type of oja allows a cylin-

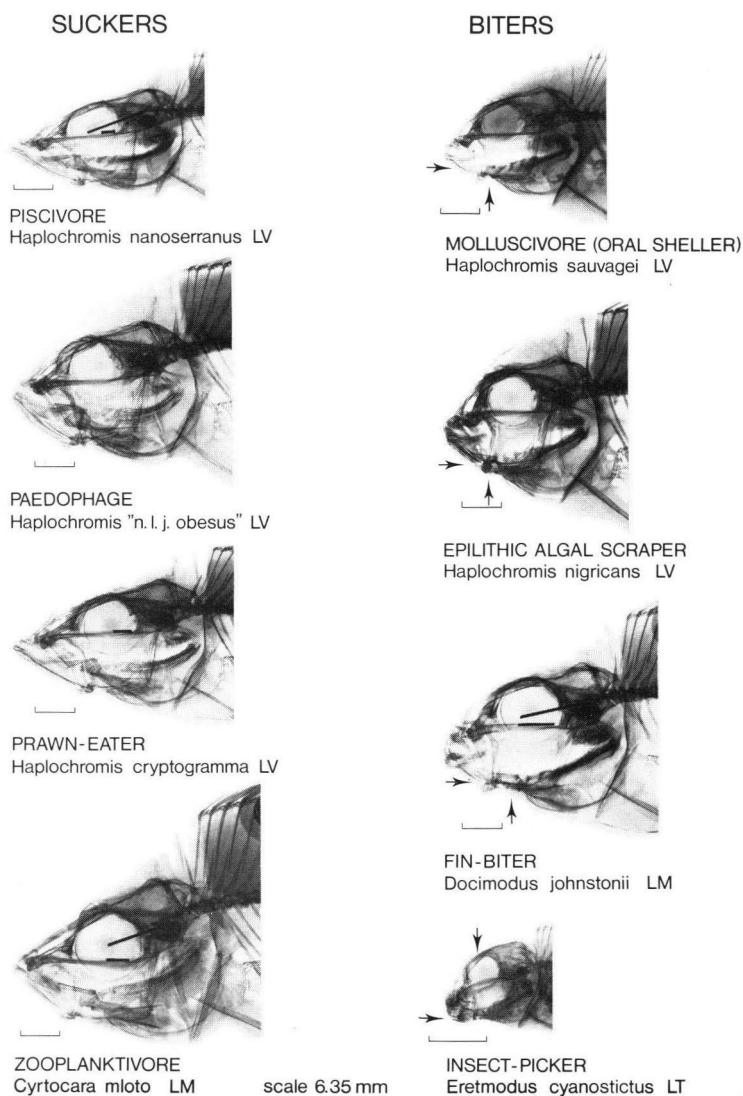


Fig. 15. Radiographs illustrating the differing positions of the hyoid symphysis of suckers compared to biters. The position of the symphysis in biters is indicated by arrows. All heads are adducted: *i.e.* mouth closed, suspensorium and gill cover adducted. The illustrated radiographs are a small sample from the many available X-rays taken from adducted heads of biters and suckers (covering many species and often a number of specimens of one species). All demonstrate the same trend: *viz.* the elevated hyoid symphysis in suckers reaching the buccal roof and the lower position in biters.

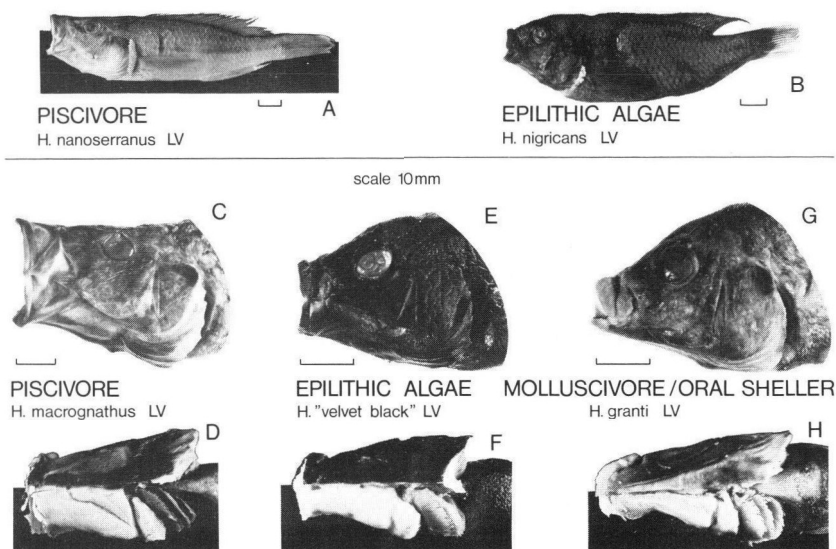


Fig. 16. Maximally expanded heads of two sucker (piscivorous) and three biter species. As printed, the neurocranial lengths of the specimens in C-H are the same. In the ventral views the right half of the casts filling the buccal cavity have been exposed by removing the right oral jaws, suspensorium, interoperculum, gill-cover, and hyoid + branchiostegals.

drical buccal cavity, whereas the spatial demands of the biting type "prescribe" a conically shaped cavity or a cavity with no rotational symmetry at all. The suitability for suction feeding of both rotationally symmetrical profiles has been deductively and experimentally proven by VAN LEEUWEN & MULLER, 1983; OSSE & MULLER, 1980; MULLER *et al.*, 1982 and MULLER & OSSE, 1983. As MULLER & OSSE (1983) state explicitly, the waterflow should be measured in a frame fixed to the gape of the fish because it is only that waterflow which provides relevant information on prey movement towards the buccal cavity. The waterflow in an earth bound frame is, in this context, irrelevant. Waterflow into the mouth in a gape-fixed frame may result from three movements: swimming, head expansion and protrusion. From the work of Osse and co-workers it is evident that swimming and/or protrusion are two ways of diminishing the contribution of head expansion to the power creating a waterflow into the mouth. Protrusion is an efficient and effective way for decreasing the prey-predator distance. Hydrodynamically, protrusion is only the lengthening of a thin-walled hemicylinder formed by both premaxillae. The resulting waterflow into the mouth is obtained with little or no impulse added to the water

(*velocity suction* of OSSE & MULLER, 1980) which diminishes the chance of the prey detecting the predator through water movement around the prey (VAN LEEUWEN, *in prep.*). The power needed for the waterflow not resulting from protrusion should be obtained from the expansion musculature (mainly the epaxial and hypaxial muscles). In suction combined with fast swimming also little impulse is added to the water. Here it is mainly the locomotory speed that makes water (with the prey) flow into the mouth. Neither protrusion nor a powerful expansion apparatus are needed (see further p. 402).

Related to the required biting force, protrusion is reduced or virtually absent in biters. Consequently their only way to reduce the contribution of head expansion in creating a waterflow into the mouth would be fast swimming. However, the streamline requirements on the outer head shape of fast swimming biters imply a considerable reduction in the maximum size of the oral cavity (see p. 408). It remains to be investigated whether such reduced cavities can be used in suction feeding. When biters do not swim fast (which applies to most biters), suction feeding would require a more powerful expansion apparatus (*i.e.* larger epaxial and hypaxial muscles) than suckers which do not swim fast but have protrusion. Suction-feeding in (non-fast swimming) biters would thus be more expensive than in (non-fast swimming) suckers. The supposed hydrodynamic relations between the relative size of the expansion musculature, swimming speed and protrusion are corroborated by the correlation between the size of the supraoccipital crest (as an expression of the epaxial and thus expansion musculature) and protrusibility, plus swimming speed (for the crest-size see fig. 22). An advantage of the cone-shaped expanding cavity (compared to the cylinder) is the feasibility to manipulate the volume flow, *i.e.* to adapt it to the type of prey sucked in (MULLER & OSSE, 1983).

The chance of prey-escape is decreased when the mouth is closed rapidly, and provided that due to such closure the waterflow is not reversed. In a cone-shaped cavity, water is pushed by the closing jaws in the right direction: towards the widest (*i.e.* caudal) section (MULLER & OSSE, 1983). The powerful (adductor) muscles required for rapid closing are a characteristic of the biting type of oJA. Besides its possibly higher energy-demand, a further *disadvantage* of the conical cavity is the smaller gape, which would allow only smaller prey to be sucked in.

The foregoing analysis demonstrates that with rotational symmetry as a hydrodynamic optimization demand, there are for many biters no morphological constraints to combine suction feeding with biting. Examples of biters which also suck small prey are the epilithic algae scrapers and other Mbuna species from Lake Malawi which also feed

on zooplankton when it is abundant near the rocks (McKAYE & MARSH, 1983; RIBBINK *et al.*, 1983), *Haplochromis* "pseudonigricans" LV scrapes algae and also feeds on phytoplankton (WITTE & WITTE-MAAS, and GOLDSCHMIDT, *pers. comm.*), and the lepidophage *Perissodus hecqui* LT which, according to LIEM & STEWART (1976), feeds predominantly on scales and, according to POLL (1956), takes zooplankton. Among the lepidophages of Lake Tanganyika, *P. hecqui* seems to have the least specialized biting apparatus. It has not the highly reduced pharyngeal jaw apparatus of the other scale-scrapers and, compared with these, possesses a relatively well-developed supraoccipital crest and relatively long fibres in the adductor arcus palatini muscle (LIEM & STEWART, 1976). Judged from a radiograph the hyoid of *P. hecqui* is of normal length and not very short as it is in *P. paradoxus* LT and *P. microlepis* LT. Whether the morphological 'specializations' for biting of the majority of the Tanganyika lepidophages exclude suction feeding remains to be investigated (see further discussion on p. 408).

Most probably many more examples of biting *plus* suction feeding will be discovered when feeding under natural circumstances is investigated more consistently.

In summary: the *sucking-type* of OJA allows a cylindrically shaped oral cavity with both protrusile and non-protrusile jaws. These possibilities result in an effective sucking mechanism for either large or small preys, but exclude feeding in which powerful biting is needed. The *biting-type* of OJA allows a cone-shaped cavity or a cavity with no rotational symmetry at all, protrusion is reduced or virtually absent and the gape is relatively small. These possibilities allow forceful biting and (in at least the case of a cone) sucking of small preys, but this sucking is more expensive than that of suckers.

Oral Jaw Apparatus, Expansion Apparatus and Gill Apparatus: Spatial Relations

The ventrad displacement of the hyoid is constructionally the result of the mediad extension of the mAM. This lower position in turn affects the position of the ceratobranchials and thus, as will be explained below, the shape of the gills. For the following reasons the positions of the ceratobranchials are more oblique in biters than in suckers (where they run approximately horizontally, fig. 15):

1) With regard to the parasphenoid bar the position of the cerato-epibranchial articulation is virtually the same or more dorsal in biters as compared with suckers.

2) The relative length of the ceratobranchial is the same or, exceptionally (2 out of 18 species), longer in suckers: 49-65% of the neurocranial length (NL) for 18 sucker-species and 48-58% NL for 14 biter-species. The two longer ceratobranchials (of suckers) reinforce the transformation-effects discussed here.

3) Both the ventrad shift of the suspensorium-hyoid articulation and the more horizontal (or even ventro-rostrad) direction of the hyoid in biters contribute to a more ventrad position of the hyoid symphysis and thus to a more oblique direction of the central axis with which the gill-arches articulate ventrally (for basic anatomy see BAREL *et al.*, 1976).

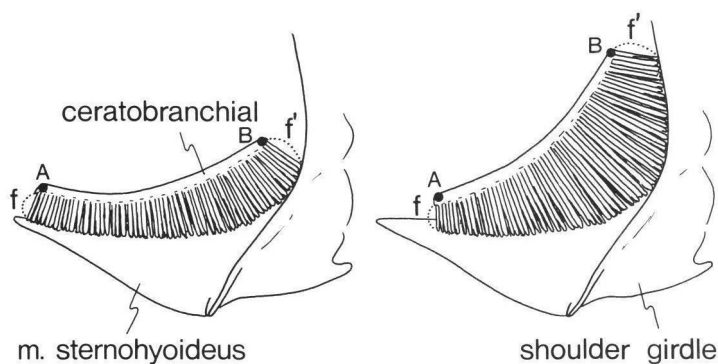


Fig. 17. Effect of the ceratobranchial position on the lengths of its gill-filaments. The length of the ceratobranchial (AB) and of its terminal filaments (f, f') as well as the border-lines with the m. sternohyoideus and shoulder girdle are the same in both figures.

Up to a certain value a more oblique position of the ceratobranchial implies a greater size in the area bordered by the ceratobranchial, the shoulder-girdle and the sternohyoid muscle, and thus more space for the ceratobranchial gill-filaments which occupy this area (fig. 17). The mean length of these filaments is indeed longer in the biters: 12-18% of the neurocranial length (NL) for 12 biter-species and 7-12% NL for 16 sucker-species (data on filament-lengths taken from GALIS & BAREL, 1980). Whether this difference in filament length is due only to the position of the ceratobranchials or is also a result of a difference in the form of the sternohyoid-muscle and shoulder-girdle, remains to be investigated.

Outer Head Shape (OHS): Form-Function Relation

Both in lateral and ventral aspects the head-profile of biters appears more obtuse than those of suckers (fig. 18). For the same neurocranial

length (NL) there is thus more space in the heads of biters than of suckers. The *constructional* relation of the differences in size and shape of this space with included structures like the oral jaw apparatus, the expansion apparatus, the gill apparatus, the eyes and the inner ear has been or will be discussed. The *functional* significance of the OHS as an arbitrarily distinguished part of the locomotory apparatus requires another reference measure, *i.e.* the standard length (SL), instead of NL. In this *functional* context the differences of the OHS observed in the constructional context are still present but less prominent (compare figs. 19 and 20).

Based on WEBB (1982) I distinguish for cichlids three types of *swimming* and for each a corresponding (body + head) profile; in addition I recognize a fourth locomotory type -place bound manoeuvring- plus its correlated body shape:

1) *Steady (time independent) swimming* requires a good anterior streamline and a minimum body area. Both conditions are found, for instance, in pelagic piscivores of the various lakes, the prawn-eating, and the as yet undescribed pelagic zooplanktivorous haplochromines of Lake Victoria. In the OHS the demands on form are reflected in small widths and depths (figs. 19, 20).

2) *Unsteady (= time dependent) swimming: acceleration only*: requires a large laterad facing body area around the centre of mass. Such deep, spindle shaped bodies are characteristic of the ambush hunting piscivorous cichlids (fig. 21) which obtain their prey by short, sudden lunges (LIEM, 1978 and *pers. obs.*). The head, as a part of the spindle, is deeper than in steady swimmers but is still acutely tapered rostrad. Mass impedes acceleration, and is reduced by *e.g.* a relatively narrow head width of the suckers.

3) *Unsteady swimming: acceleration plus turning*. If in addition to acceleration, turning is required, a large body depth along a greater extent of body length becomes favourable. Snout-engulfing paedophages have such locomotory requirements (*cf.* WILHELM, 1980). The extension of the area of greater depth involves mainly the supraoccipital area of the head (fig. 21).

4) *Place-bound manoeuvrability*. Place-bound manoeuvring is rotation only, *i.e.* yaw, pitch and/or roll without translation. This type of movement plays the dominant role in the locomotion of substrate feeders (*e.g.* pitch in epilithic algae scrapers and most likely in oral shelling molluscivores). Following ALEYEV (1977) a round dorsal profile plus a flat ventral outline would be an adaptation to pitch as it allows efficient rotation over an arc. Such round dorsal profiles (especially the OHS) are characteristic of many epilithic algae scrapers (fig. 21) and oral shelling molluscivores. As long as acceleration plays

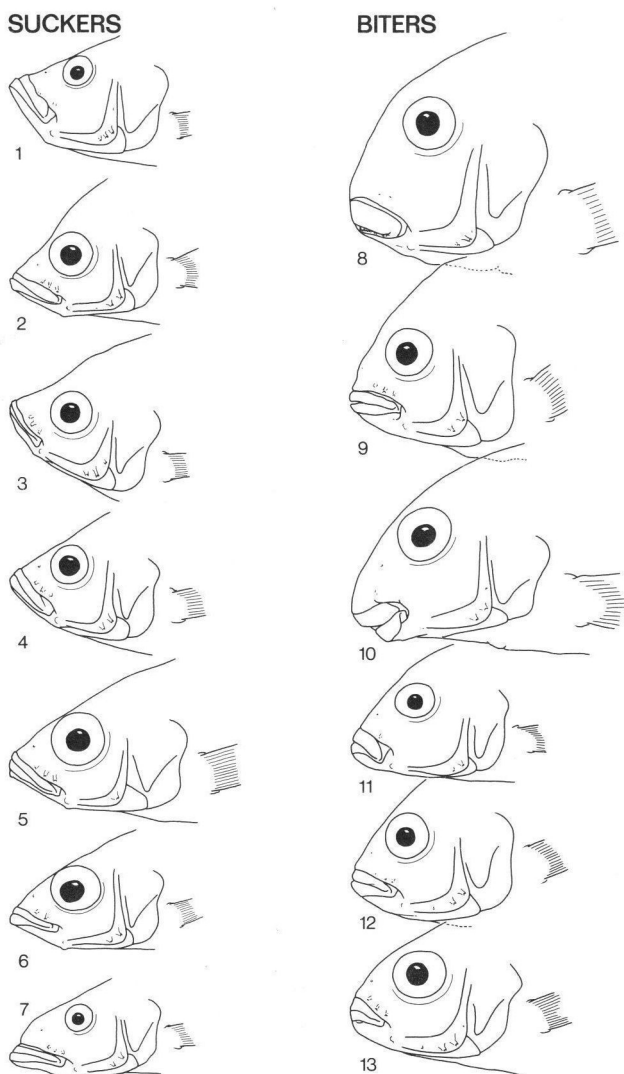


Fig. 18. Lateral and ventral view of the head profiles of biters and suckers.

a minor role, mass is not so important. This might help to understand the permissibility of the greater head (and body) width of the biters (figs. 19, 20). For most (all?) lacustrine cichlids the greatest section of the body and head surface is directed laterad. This, combined for most biters with a relatively deep body area over a great extent of the body

SUCKERS



1 *H. plagiostoma* LV
PISCIVORE: AMBUSH HUNTER



2 *H. microdon* LV
PAEDOPHAGE: PURSUIT HUNTER?



3 *Cyrtocara mloto* LM
ZOOPLANKTIVORE



4 *H. 'pink paedophage'* LV
PAEDOPHAGE: SNOUT ENGULFER



5 *H. 'erythrope'* LV
PISCIVORE: PURSUIT HUNTER



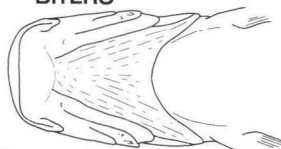
6 *H. 'argens'* LV
ZOOPLANKTIVORE



7 *H. dentex* LV
PISCIVORE: PURSUIT HUNTER

scale = 10mm

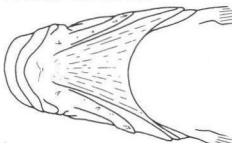
BITERS



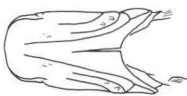
8 *Tropheus* sp. LT
ALGAE SCRAPER



9 *H. nigricans* LV
ALGAE SCRAPER



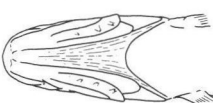
10 *Eretmodus cyanostictus* LT
INSECT-PICKER



11 *Genyochromis mento* LM
SCALE-SCRAPER



12 *H. sauvagei* LV
MOLLUSCIVORE: ORAL SHELLER



13 *Docimodus johnstoni* LM
FIN-BITER

length, serves acceleration and turning (see above): except for a negative effect of their greater mass, place-bound manoeuvring fishes would also be well adapted to make sudden darts and turns. This capacity is important when it is necessary to flee from predator: *e.g.* when 'epilithic algae scrapers', feeding on zooplankton in the open water, have to seek shelter in the rocks.

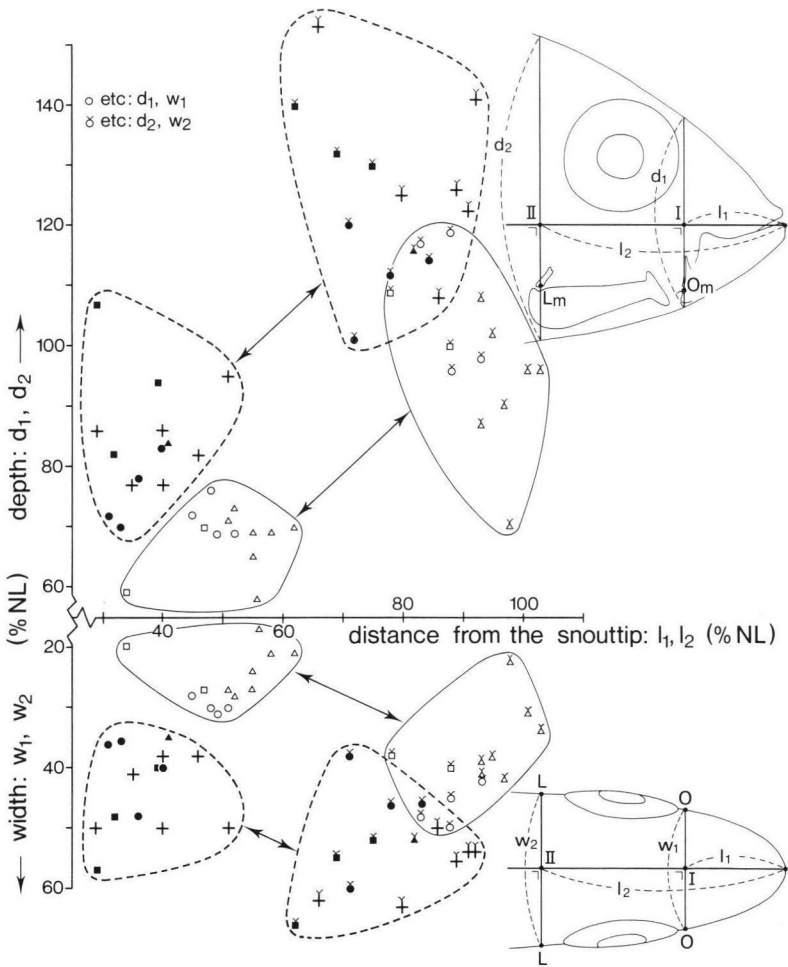


Fig. 19. Differences in the head profiles of biters and suckers measured at two transverse levels with the neurocranial length (NL) as a reference measure. The horizontal line I-II runs parallel to the parasphenoid. Lm and Om are the mediad projections of the hyoid-interhyal articulation (L) and lower-jaw-suspensorium (O) articulation, respectively. Other symbols and conditions as in fig. 4.

*Expansion Apparatus (EA) and Locomotory Apparatus
(Including Outer Head Shape - OHS)*

Expansion apparatus and outer head shape: spatial relations

The size differences in the supraoccipital crest are reflected in the outer head shape (OHS) and thus in the total profile of the fish. The

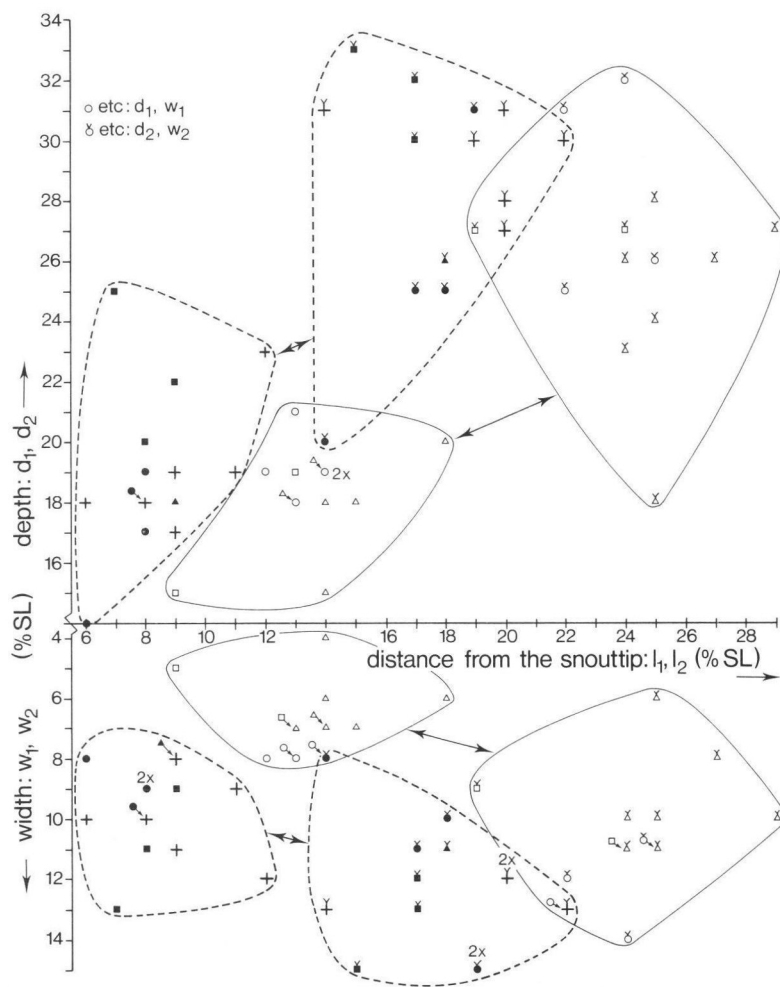


Fig. 20. Same as fig. 19, but with the standard length (SL) as a reference measure.

functional significance of these crest-sizes is discussed on p. 380. Increase in crest size is first correlated with an increase in body depth over a restricted area of the body length and then with a mainly rostrad increase of this area of greater depth (compare figs. 21 and 22). The locomotory significance of the various body profiles was discussed above. Care should be taken not to reverse the spatial relation noted above. Fishes with deeper (more curved) head profiles do not necessarily use that space to accommodate larger expaxial muscles, as

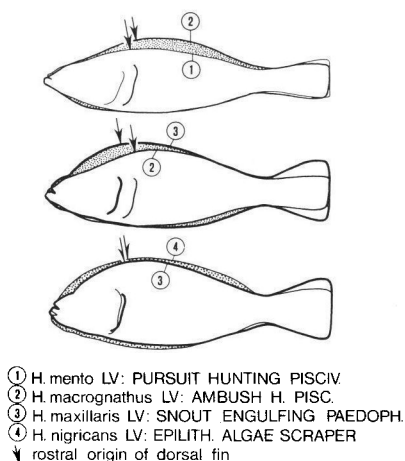
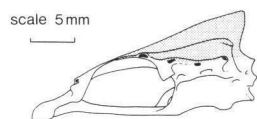
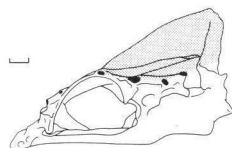


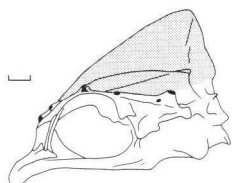
Fig. 21. Contour outlines of the lateral profiles of haplochromines presumably differing in locomotion types with the standard or total length as a reference measure.



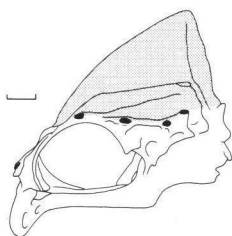
SWIMMING: FAST & STEADY
 (CRUSTACEAN-EATER ?)
H. sulphureus LV



SWIMMING: ACCELERATION
 (AMBUSH HUNTING PISCIVORE)
H. plagiotoma LV



SWIMMING: ACC. & TURNING
 (SNOUT-ENGULFING PAEDOPHAGE)
H. obesus LV



PLACE BOUND MANEUVERING
 (ORAL SHELLING MOLLUSCIVORE)
H. prodromus LV

Fig. 22. Neurocrania of haplochromines presumably differing in locomotion types. As figured the neurocranial lengths are the same. (Neurocrania redrawn from GREENWOOD, 1974 and GREENWOOD & BAREL, 1978).

will be demonstrated in the section where the size of the inner ear is taken into account (p. 392).

The hypaxial muscles have not been investigated completely. Preliminary results of comparative studies by H. Bos (*pers. comm.*) indicate that the pectoral region of biters compared to suckers is often deeper (relation with body depth → with locomotion) and wider (related with difference in head width → with biting). The greatest

width and depth of a cichlid fish are found approximately at the level of the paired fins, *i.e.* in the pectoral area. As for hydrodynamic reasons there is no abrupt change in profiles, it is not unexpected that the greater head widths and often greater head depths of the biters (fig. 19) also result in a greater width and depth at the level of the paired fins. Constructionally this implies (among others) a larger space for the pectoral muscle bloc, which contains the pelvic, pectoral and hypaxial muscles: the ratio (*cube root volume muscle bloc*)/(*neurocranial length*) is 12-17‰ for 9 sucker species and 17-20‰ for 6 biter species (H. Bos, *pers. comm.*). Within this muscle bloc as a constructional com-

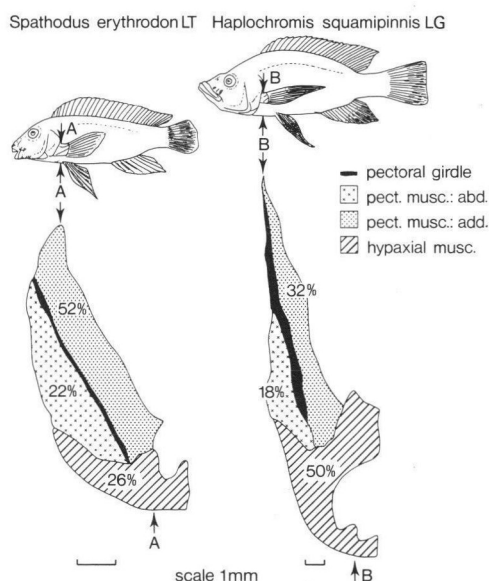


Fig. 23. The relative (percentage of total cross-section) contribution of the various muscles in the pectoral muscle bloc of a biter (*S. erythron*) and a sucker (*H. squamipinnis*). Note that this is another constructional context than that generally used in this paper. From this context alone no direct functional inferences can be made.

ponent, the pectoral fin muscles dominate in the biters, whereas in suckers the hypaxial muscles are dominant over or of the same volume as the pectoral fin muscles (fig. 23). Compared with neurocranial length (*i.e.* the reference measure of the constructional component mostly considered in this paper), the cube root of the hypaxial-muscle-volume of biters is larger than those of suckers or (less frequently) overlaps the higher values of suckers. The biters investigated so far only comprise algae scrapers and insect pickers.

Expansion apparatus and outer head shape: constructional morphology

If suction feeding is needed, then the locomotion series given in figs. 21, 22 coincides with an increased need of power for head expansion, e.g. for an increase in the size of the hypaxial and the epaxial musculature. During fast swimming, water movement into the mouth results from locomotion speed. There is no need for powerful head expansion nor would the required shallow body depth accommodate large epaxial muscles. In ambush hunting the rôle of head expansion in creating a suction flow is increased. The head depth (and with it the space for the epaxial muscles) is also increased due to locomotory requirements. In the step "*ambush hunting piscivore*" → "*snout engulfing paedophage*" the need for head expansion for suction is likely to have increased further; again this correlates with the understandable (in terms of locomotion) rostro-dorsad increase in head depth and thus in space for the epaxial muscles. As was argued on p. 380 the reduced protrusion of biters, if combined with a low swimming speed (or no swimming at all), calls for well-developed expansion muscles. The epaxial component of this musculature can be accommodated in the deep and rounded dorsal head profiles of place-bound manoeuvring biters and -concerning the hypaxial musculature- in the larger pectoral area (see above). Functionally the larger pectoral muscles of the few algae scrapers and insect pickers investigated so far seem to be correlated with a higher and more permanent demand on manoeuvrability (algae scraping from variously inclined rock-surfaces or food collecting among pebbles in a highly turbulent habitat) but a more precise, quantitative relation between these demands and the structure of the pectoral fins plus their muscles remains to be investigated. Functionally the greater width and depth of the body at the insertion of, respectively, the pectoral and pelvic fins also means an increase in the arm of the turning force resulting from movement of these fins.

*Outer Head Shape (OHS) and Oral Jaw Apparatus (OJA)**Outer head shape and oral jaw apparatus: spatial relations*

Compared with suckers the broader adductor muscles of biters should be accommodated by mediad and/or laterad extension. The mediad extension has not been investigated for all specimens but from dissection I gain the impression that the space between the parasphenoid and the dorsal border of the suspensorium is narrower in the biters, which could imply mediad broadening of the adductors (fig. 12). Laterad extension certainly plays a rôle: biters have broader heads than suckers (fig. 19). Broader head plus shorter jaw lengths have

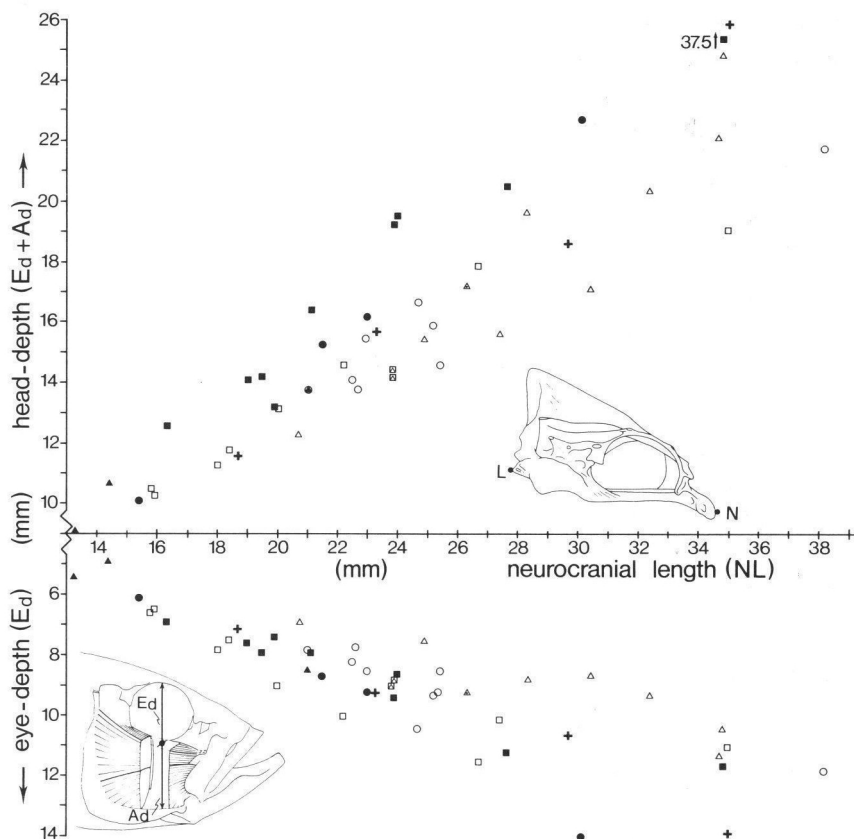


Fig. 24. Contribution of eye-depth (Ed) and the depth (Ad) of the m. adductor mandibulae to the head-depth (Hd) of biters and suckers. The neurocranial length (NL) is the reference measure. Symbols and conditions as in fig. 4.

cumulative effects on the angle between the rami of the lower jaws. It ranges from 38° - 87° in the biters and 15° - 37° in the suckers (many species investigated), thus even for suckers and biters with the same relative jaw length the angle in biters is larger*. Functionally the wider angle provides the biters with a more effective (broader) grasp, which is especially relevant for scraping algae and scales from flat surfaces.

The head-depth (Hd) at the level of the muscle depth measurement is mainly** determined by the muscle depth (Ad) plus eye depth (Ed).

* Note that the reverse - a wider angle implies a broader head - does not hold because the shorter jaws as in most biters would also result in a wider angle at the same head width.

** The contributions from the preoperculum, interoperculum and supraoccipital crest are neglected.

As biters may have a larger Hd than suckers, but do not differ in Ed, larger Hd's are mainly related to larger Ad's (fig. 24).

A powerful biting-force requires a relatively short premaxillary process at a large angle to the dentigerous arm, and a decurved ethmoidal area (*cf.* OTTEN, 1983). These factors together with the larger angle between the mandibular rami contribute to the three dimensionally more obtuse snout-profile of the biters. The more acute profile of suckers (fig. 18) can be related to the functionally determined structure of their oral jaws.

Outer head shape and oral jaw apparatus: constructional morphology

At least in part, the differences in OHS can be explained (*constructionally*) by differences in the concomitant oJA's. Where suckers and the place-bound manoeuvring cichlids are concerned, there is no conflict between the functional demand on the structures and their spatial relations. The sharper and (in ventral aspect) narrower profiles of the OHS of suckers, as well as the more rounded and (in lateral aspect) deeper profiles of the OHS of biters (figs. 18, 19) are adaptations to their locomotory requirements. The broader head-width of the biters (as an expression of increased mass) seems admissible in place-bound manoeuvring (see above). The greater angle between the rami of the lower jaws of biters is a spatial consequence of head widening to accommodate the broader mAM; functionally a greater jaw width implies a better grasp on broad or flat objects (*e.g.* a rock from which algae must be scraped). As can be derived from the foregoing, a conflict between function and spatial demand arises when biting is to be combined with fast swimming (see p. 408).

Outer Head Shape and Inner Ear: Spatial Relations

An increased depth in head profile does not necessary imply more space for the epaxial part of the expansion musculature. There are apparently other structural and positional means resulting in such profiles: *e.g.* the oral shelling molluscivore *Haplochromis xenognathus* LV and the insect-picker *Tanganicodus irsacae* LT which can both be classified as biters on the basis of their oJA, have similarly (moderately*) curved dorsal head profiles. However, whereas *H. xenognathus* has a large supraoccipital crest, the crest is only very weakly developed in *T. irsacae* (fig. 25). Still in both species the neurocranium is the *main* support of the dorsal region of the head profile. The lower depth of the supraoccipital crest is "compensated" by: (1) a relatively thick layer of

* For a definition of this qualification see BAREL *et al.* (1977).

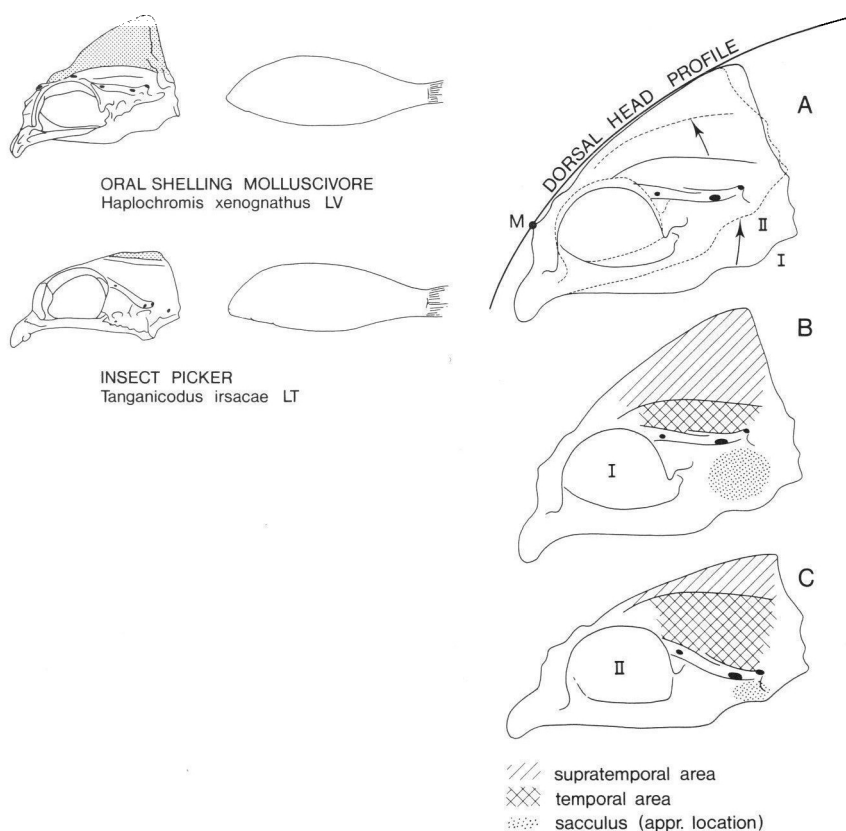


Fig. 25. Outlines and neurocrania of two biter-species (lateral view). Note how differently shaped neurocrania support similarly shaped (*viz.* moderately decurved) head profiles. Dotted area: supraoccipital crest. (Neurocrania redrawn from GREENWOOD, 1974 and LIEM, 1979).

Fig. 26. Theoretical transformation of the neurocranium (I) of *H. xenognathus* LV to a neurocranium (II) like that of *T. irsacae* LT. The transformation is obtained by (1) rotating neurocranium I around point M, (2) keeping its dorsal outline inside the illustrated head-profile by decreasing the depth of the supraoccipital crest and (3,4) leaving the ethmovomerine bloc and the lateral line crest in the original position. Compare C with the real neurocranium of *T. irsacae* illustrated in fig. 25. The figure is further discussed in the text.

fatty tissue between crest and epidermis in *T. irsacae* and (2) tilting of the neurocranium. Because the lateral line crest contains the horizontal semicircular canal (fig. 27), the intracranial¹ (clockwise in figs. 25, 26) rotation of this crest in *T. irsacae* can be conceived of as a structural

¹ Measured with regard to *neurocranial* horizontal defined through the parasphenoid.

correction for the extracranial² (counter-clockwise in figs. 25, 26) rotation of the whole neurocranium¹. Concomitant with the crest-rotation is the increased depth of the temporal area, which accommodates the vertical semicircular canals (fig. 27). Compared with haplochromines, the temporal and supratemporal fossae of *T. irsacae* are shallow, *i.e.* the fossa floor seems to have extended outward, thus creating a larger cranial cavity and decreasing the space for the epaxial muscles. From these observations on external form differences in the otic area it seems that *T. irsacae* (and probably also *Spathodus* and *Eretmodus*) have increased the space for the semicircular canals at the cost of space for the sacculus and lagena (judged from radiographs the otoliths are small) and at the cost of the accommodation and insertion of the epaxial musculature on the *dorsal* side of the neurocranium. Judging from

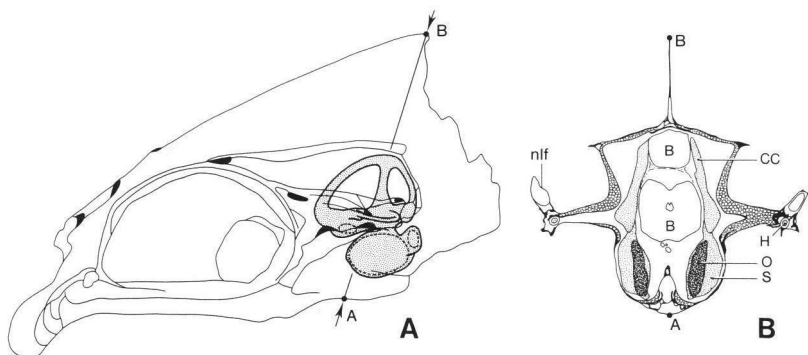


Fig. 27A. The inner ear in the neurocranium of *Haplochromis elegans* L.G. B. Cross-section approximately at the level AB indicated in A. Legend: B = brain, CC = crus commune, H = horizontal semicircular canal, nlf = neurocranial lateral line foramen, O = otolith, S = sacculus. (A is a reconstruction made by G. Ch. Anker from serial sections).

radiographs, a neurocranium similar to those of the three Tanganyika genera is found in the insect-picker *Labidochromis maculicauda* LM, which also has a similar lower jaw (fig. 3). Whether in these species the epaxial musculature and its function in head expansion is reduced remains to be investigated. The reduced swim-bladder and the lower position of the articulation between the vertebral column and the neurocranium in *T. irsacae* makes comparison with other lacustrine cichlids difficult.

² Measured as the inclination of the neurocranial horizontal with regard to the absolute horizontal (H) through the caudal section of the lateral line (see BAREL *et al.*, 1977).

Suction feeding *per sé* is not excluded, as was demonstrated in tanks for *Eretmodus cyanostictus* LT and *Spathodus erythron* LT (LIEM, 1979).

The increase in space for these semicircular canals (which give information on the degree of positional change of the fish) is correlated with their occurrence in a highly turbulent environment of the surf-zones of Lake Tanganyika. However, as the comparisons have been made in a constructional context only, the functional significance remains to be investigated: *e.g.* it is not known what absolute size of the semicircular canals a proper functioning requires (*T. irsacae* is a small cichlid!).

When the functional significance of the inner ear of cichlids is better understood, the constructional relationships of this relatively large sense organ (fig. 27) with the form and function of other head apparatuses will be a fruitful field for research, especially because the size and position of sense organs in general seem to exert a particularly dominant demand on head construction (DULLEMEIJER, 1974).

Pharyngeal Jaw Apparatus (PJA) and Expansion Apparatus (EA)

Pharyngeal jaw apparatus and expansion apparatus: spatial relations

The pharyngeal jaw apparatus (PJA) is defined as the branchial skeleton, its ligaments and muscles. In cichlids the PJA forms a set of jaws additional to the oral jaws; *i.e.* the PJA not only serves in the transport of food into the esophagus (as in most fishes) but is often well-adapted to triturating food, thus freeing the OJA from this task. Gradual morphological series of PJA's can be made; examples are found in BAREL *et al.* (1977: fig. 58) for interspecific variation in the shape and dentition of the lower pharyngeal jaw (LPJ), and in HOOGERHOUD & WITTE (1981) for intraspecific diversity. Functionally the LPJ-series may run from “*transport of small items (e.g. algae) into the esophagus only*” through “*lacerating prey (e.g. fish)*” to “*crushing hard prey (e.g. molluscs)*”. This changing mechanical demand is reflected in form-differences of all elements of the PJA and in the increasing relative size of the PJA. HOOGERHOUD & BAREL (1978) analysed the effect of this size-increase on the EA by comparing (pharyngeal) mollusc-crushers and piscivores of Lakes Victoria and George. The two trophic PJA-types differ conspicuously in size. The enormous size increase of the molluscivorous PJA involves expansion in virtually all directions and, compared with the piscivores, has among others the following effects on the surrounding elements (fig. 28): *Laterad*: flattened m. protractor pectoralis with a long tendon (not figured). *Rostrad*: constriction of the space between the eye and the PJA: the origin (post-orbital wing) of the m. levator arcus palatini is less developed. *Ventrad*: decrease in cross-section and

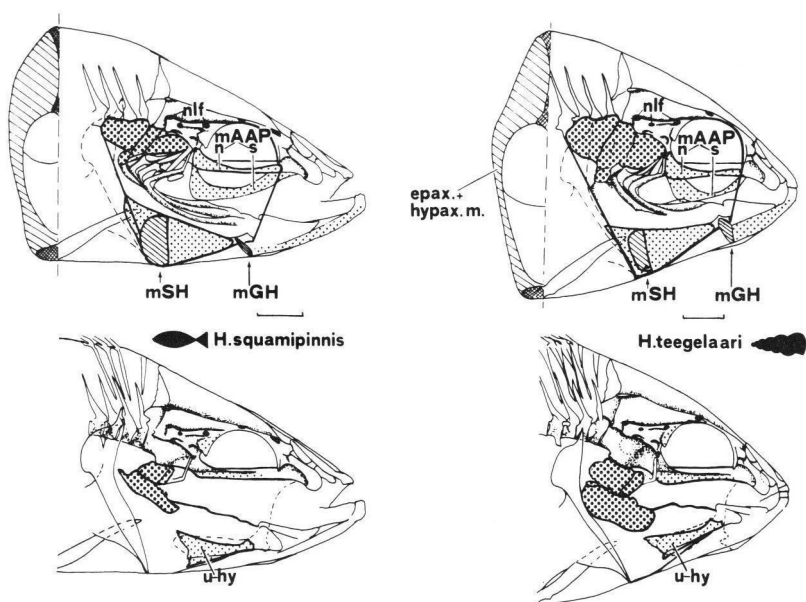


Fig. 28. Main pharyngeal (heavier grid) and expansion (lighter grid) muscles and skeletal elements of the piscivorous *Haplochromis squamipinnis* LG and the pharyngeal mollusc-crusher *H. teegelaari* LV. Legend: epax. + hypax. m. = epaxial + hypaxial musculature, mAAP = m. adductor arcus palatini, mGH = m. geniohyoideus, mSH = m. sternohyoideus, n = neurocranial insertion area of mAAP, nlf = three caudal neurocranial lateral line foramina, s = suspensorial insertion area of mAAP, sb = swim bladder, u-hy = urohyal, vc = visceral cavity. Hatched areas are the cross-sections of muscles drawn in the plane of drawing. (Adapted from HOOGERHOUD & BAREL, 1978).

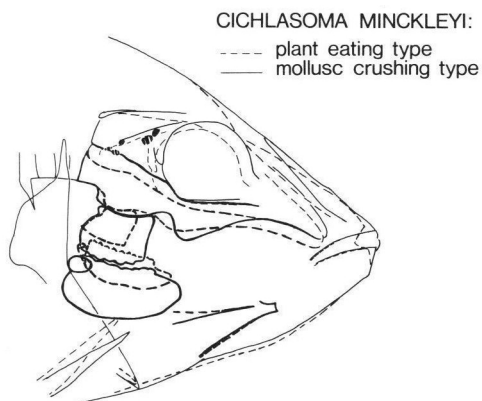


Fig. 29. Size differences in the pharyngeal jaws and urohyal of two morphs of *C. minckleyi* from the Cuatro Ciénegas basin in Mexico. (Adapted from HOOGERHOUD & BAREL, 1978).

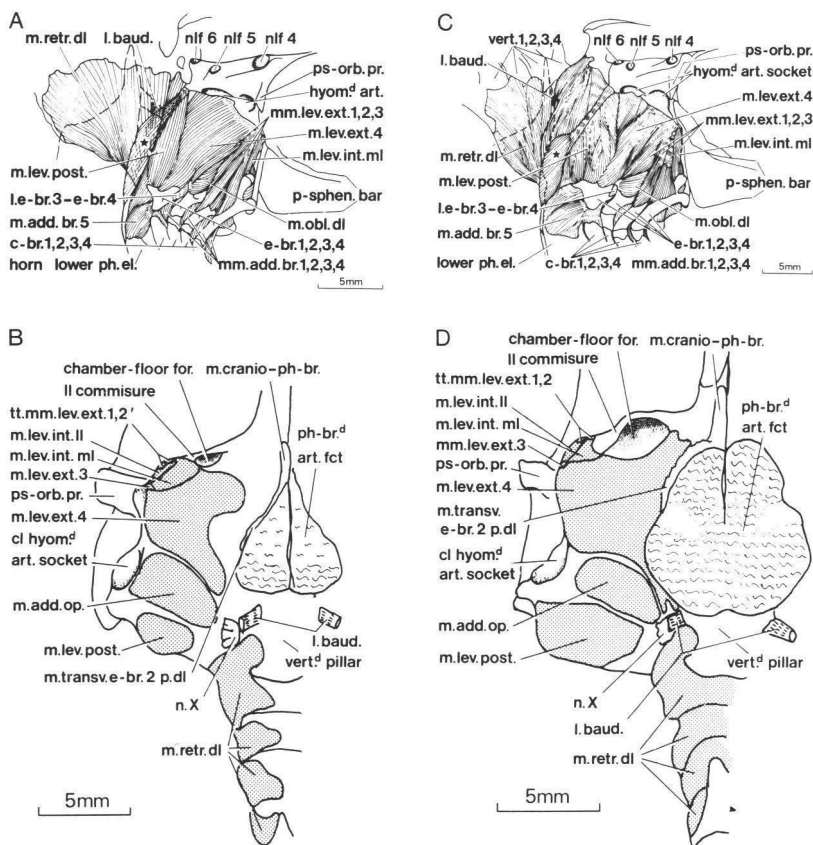


Fig. 30. Upper pharyngeal muscles of two morphs (plant eater A, B and mollusc-crusher C, D) of *Cichlasoma minckleyi* from the Cuatro Ciénegas Basin in Mexico. A, C: lateral view. B, D: ventral views of the insertion areas on the neurocranium. **Legend:** cl.hyom^d. art = caudal hyomandibulad articulation, e-br. = epibranchial, for. = foramen, l. = ligament, ll = ligaments, m = musculus, mm = muscoli, mm. add.br. = mm. adductores branchiales, m.add.op. = m. adductor operculi, m.cranio-ph.br. = m. cranio-pharyngobranchialis, mm.lev.ext. = mm. levatores externi, m.lev.int.ml.ll. = m. levator internus medialis lateralis, m.lev.post. = m. levator posterior, m.obl.dl. = m. obliquus dorsalis, m.retr.dl. = m. retractor dorsalis, m.transv.e-br. 2 p.d.l. = m. transversus epibranchialis 2 pars dorsalis, nlf = neurocranial lateral line foramen, n.X = nervus X, ph-br.^d art.fct. = pharyngobranchiad articulation facet, ph.el. = pharyngeal element, ps-orb.pr. = postorbital process, p-sphen. = parasphenoid, tt = tendons, vert. = vertebral, vert.^d = vertebrad., * = m. protractor pectoralis. (Drawn by R. J. C. Hoogerhoud).

ventrad displacement of the m. sternohyoideus. *Mediad and caudad*: decrease in the head-kidney size. *Internal*: constriction of the corridor for the m. adductor operculi (WITTE & BAREL, 1976). Inverse relation between the size of the insertion areas for the m. levator internus versus the area for the m. levator externus.

Within the polymorphic species *Cichlasoma minckleyi* (described by KORNFIELD & TAYLOR, 1983) from Cuatro Ciénegas, the same effects are observed in specimens with larger PJA's (figs. 29, 30).

The muscles which are "affected" by the PJA-size belong to the expansion apparatus (EA). Subsequently other "expansion-muscles" not directly bordering the PJA were investigated, *i.e.* the rostral part of the epaxial muscles (levating the head) and of the hypaxial muscles (retracting the shoulder girdle). With allowance made for differences in neurocranial lengths, the epaxial and hypaxial muscles demonstrate the same trend as the intracranial muscles discussed above. In cross-section the extracranial muscles of the expansion apparatus are larger in piscivores than in molluscivores. The spatial (and consequently functional) effects on the abdominal cavities have been discussed by HOOGERHOUD & BAREL (1978).

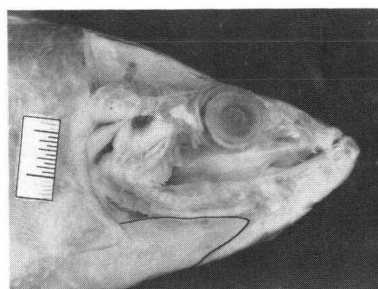
Pharyngeal jaw apparatus and expansion apparatus: constructional morphology

Provided that the constructionally observed relations are also of functional significance, the inverse relation between the size of the PJA and the size of the muscles operating the EA seems a plausible adaptation to the two feeding habits through internal reorganization. Piscivores obtain their large and fast prey by sucking it into the mouth. For this a powerful (and consequently large) EA is necessary when ambush hunting predators are concerned. In pursuit-hunters the required streamline affects the EA (see p. 386 for the effect of OHS on EA). The comparatively soft fish-prey can be triturated by a relatively small-sized PJA. The small, inert snail prey may be sucked in by an EA of less capacity, but crushing this hard prey demands a powerful and consequently voluminous PJA. As pharyngeal mollusc-crushers also have a relatively well-developed protrusion, their suction apparatus cannot be directly compared with those of biters.

The foregoing strongly suggests an inverse and trophically understandable relation between the size of the EA and the size of the PJA. The validity of this suggestion has been strengthened by extending the comparison to the snout-engulfing paedophages. Among the approximately twenty species predating on cichlid eggs and larvae (called paedophages by GREENWOOD, *e.g.* 1974), a number presumably obtain their prey by engulfing the snout and subsequently sucking the brood from the buccal cavity of a brooding female. Snout-engulfing was ac-

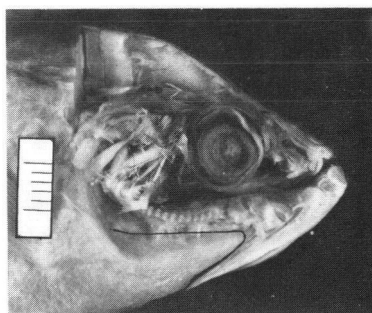
PISCIVORE

PAEDOPHAGE



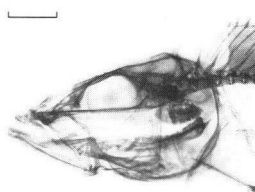
H. plagiostoma LV

A



H. "white lip obeseus" LV

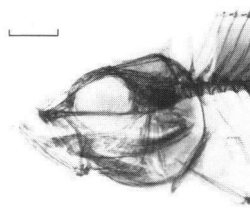
C



H. macrognathus LV

B

scale 6.35mm



H. "micro-obeseus" LV

D

Fig. 31. Ambush hunting piscivore and snout-engulfing paedophage. A, C: gill and expansion musculature exposed. Oral jaws, suspensoria, interoperculum, gill cover, hyoid, branchiostegal rays, gill-filaments and rostral section of the epaxial muscles have been removed. C, D: radiographs of adducted heads. As printed the neurocranial length in A & C and in B & D is the same. Note the larger expansion muscles (epaxial and -with marked outline- sternohyoid) and smaller gill-arch-muscles plus pharyngeal jaws in the paedophage).

tually observed for one specimen by WILHELM (1980). The extrapolation to other species is based on comparative functional morphology of the oral jaw apparatus and expansion apparatus.

As eggs and larvae are small, soft items, it is not surprising that the size of the pJA of paedophages is smaller than that of piscivores feeding on larger, free-swimming haplochromines. Preliminary anatomical comparison indicates an inverse relation between the relatively small pJA in snout-engulfers and the surrounding muscles of the EA which are enlarged* compared with those of ambush-hunting piscivores (fig. 31). It seems plausible (but remains to be proven hydrodynamically) that sucking the contents from the buccal cavity of a brooding female re-

* The enlargement of these muscles is not only accommodated by a reduction of the pJA but also by an increase in the head depth.

quires a more powerful expansion apparatus than does sucking in a free-swimming prey (the strategy of the ambush hunter).

Intratrophic Comparison of Integration of Apparatuses

The last example of spatial relations concerns an *intratrophic* comparison involving five apparatuses: OHS, OJA, EA, eye and gill apparatus. According to COULTER (1965-66) *Hemibates stenosoma* LT, *Bathybates graueri* LT and *B. ferox* LT are all piscivores feeding on cichlids and clupeids (hence *intra-trophic* comparison). Due to its occurrence in the deep hypoxic layers of L. Tanganyika (*H. stenosoma*), to an active pelagic life (*B. ferox*) or to both (*B. graueri*), the demands on oxygen extraction are high for all three species (see GALIS & BAREL, 1980).

In lateral view the entry-angle of the head-outline of *Hemibates* is more obtuse when compared with the acutely tapering profiles of the *Bathybates* spp. (fig. 32A, B). As there is no marked difference in head-width, the head volume of the *Bathybates* spp. is smaller than that of *Hemibates* and consequently at least some head structures of the *Bathybates* spp. should be smaller in size. Externally the two genera differ in the shape of the eye: elliptical ("compressed" dorsad-ventrad) in *Bathybates*, and circular in *Hemibates* (fig. 32). The relative length of the horizontal radius (the eye-length of BAREL *et al.*, 1977) is virtually the same in the three species and in absolute size represents a very large eye (at least for cichlids; BAREL & SCHULLER, *in prep.*). This correlates with the occurrence of the three species in deep water (> 70 m). The absolute (and not the relative) size of the eye is an indication of its optical capacities (OTTEN, 1981). An eye with a circular shape and the same radius as the eye of *Hemibates* would in *Bathybates* protrude dorsad and/or diminish the depth of the adductor mandibulae muscle (mAM) (fig. 32I). The interruption of the head profile would affect the streamline and is therefore undesirable. For reasons given below the "intrusion" into the mAM is also unwanted. Consequently the elliptical shape at least seems to be the result of constructional demands of the mAM and the head profile. Whether it is also of functional significance or only a compromise remains to be investigated. A similar reasoning applies to the decrease in the expansion musculature and the gill filaments. Both the epaxial and sternohyoid muscles are significantly shallower in the *Bathybates* species (fig. 32E,F) and the lengths of their gill filaments* are shorter (fig. 32C, D). The sum of these decreases contributes to a head with a shallower profile.

* *i.e.* the filaments of the ceratobranchial which constitute the larger part of the gills on a hemibranch (GALIS & BAREL, 1980).

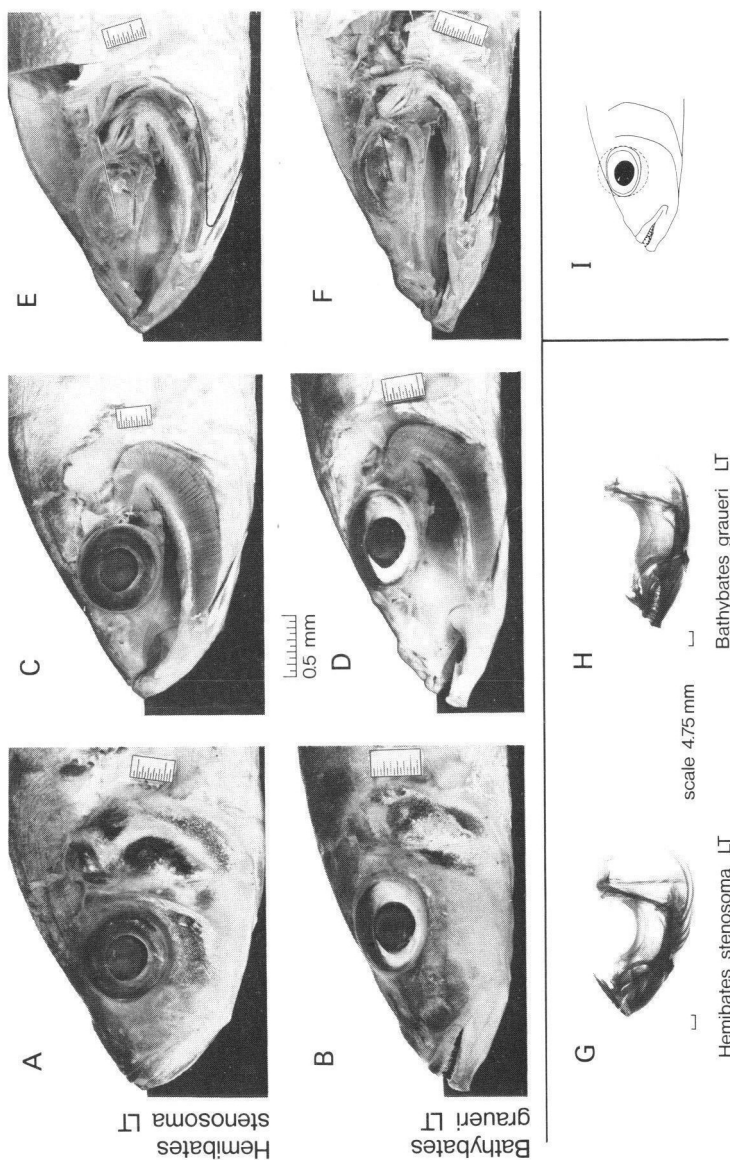


Fig. 32. The relation between head outlines and internal structures of two deep-water piscivores from Lake Tanganyika. A, B: intact head. C, D: suspensoria, gill-cover, hyoid + branchiostegals, oral jaws, circumorbitals and nasals removed from the left side. E, F: as C, D but also eyes, gill-filaments and rostral section of epaxial muscles removed from right side; m. sterno-hyoideus outline marked. G, H: radiographs of oral jaw apparatus (plus hyoid apparatus). I: outline of the *Hemibates* eye placed in *Bathybates*. In figures A-F the neurocranial lengths (NL) are the same.

However, what morphological alternatives do the *Bathybates* spp. have to solve the functional problems of a high oxygen demand and of getting food into the buccal cavity? That both muscle depth and filament length decrease seems plausible for the following reasons: the accommodation of a respiration area required for *Bathybates* with the same gill structure as *Hemibates* would increase the filament length to such an extent that virtually no space would be left for the sternohyoid muscle. The functional conflict imposed by a higher oxygen demand plus a decrease in space for the gills is probably solved structurally by the larger secondary lamellae, and further also by the relatively smaller body volume of *Bathybates*. The gill structure of *Bathybates ferox* is extreme among cichlids (GALIS & BAREL, 1980). The accommodation of a sternohyoid muscle of the size seen in *Hemibates* seems unnecessary in *Bathybates* as the waterflow probably results mainly from swimming and not from active head expansion.

On anatomical grounds the maximum volume (important for prey size) and the kinematics of the expansion apparatus in *Bathybates graueri* and *Hemibates stenosoma* seem similar, e.g. the hyoid-lengths, the distance from the hyoid-suspensorium articulation to the rotation axis of the suspensorium, the length of the buccal cavity, the length of the ceratobranchials, are all virtually the same. The considerably smaller size of the expansion musculature in *Bathybates* (constructionally due to head shape plus gill-filaments) suggests a reduced suction capacity by *head expansion*, which, as was explained on p. 379, is indeed allowed. Also, in suction feeding at high swimming speed there is no need for protrusion (VAN LEEUWEN, *in prep.*). This allows an additional (or alternative) apparatus for securing the prey, i.e. an oja with, for suckers, a *relatively* well-developed biting capacity. The index of static biting force (p. 369) is 5.5 for *H. stenosoma* and 7.9 for *B. graueri* with the same neurocranial length (44 mm). As can be seen from fig. 9 both values are low compared to biters. The greater biting force of *Bathybates* is directly or indirectly reflected in the following anatomical features:

- 1) Large teeth on premaxilla and dentary. In absolute size the *Bathybates* teeth (fig. 2) are some of the largest among piscivores. Such large teeth are also found in *Haplochromis* "big teeth" LV and *Haplochromis dentex* LV (VAN OIJEN, 1982) which also hunt for fast prey.
- 2) A relatively well-developed m. adductor mandibulae (mAM): cross-sections *ca* 14 mm² in *Hemibates** and *ca* 29 mm² in *Bathybates graueri**. Both the width and the depth of the mAM contribute to its larger cross-section in *B. graueri*. Compared with head shape the

* Specimens of the same neurocranial length: 44 mm.

biters the decurvature results from a dorsad protruding plug of the ethmoidal cartilage (fig. 33). LIEM (1978) overlooked the particular structure of the *Bathybates*-bloc (fig. 33), neither did he mention other structures in which *Bathybates ferox* deviates from the other piscivores studied by him. The *Bathybates*-form of the ethmovomerine bloc is interesting because it satisfies a combination of demands: the decurvature needed for biting, rostrad elongation of a sucker contributing to a sharp head profile and serving the accommodation of long jaws.

CONCLUSIONS, DISCUSSIONS AND PERSPECTIVES

Food-Function-Form Relations

There is no simple relation between food and form, neither in the oral jaw apparatus, nor in any other part of the feeding apparatus. The relations between the food-categories eaten and the structure of the feeding apparatus are indirect and complicated. This appears to be the result of at least two factors:

1) The feeding function of the feeding apparatus is not necessarily the only demand determining its structure: Spatial requirements of other apparatuses are often essential co-determinants, *e.g.*, among suction-feeders the structure of the oral jaw apparatus and expansion apparatus depends on the structure of the locomotion apparatus (see pp. 370ff, 386ff).

2) The functional significance of the feeding apparatus is to be understood in mechanical terms. It is the mechanical way in which food is treated that explains the structure of the feeding apparatus, food-categories are subordinate to that. In other words: the same food-category can be treated in different ways (and thus by anatomically different feeding apparatuses) and different food-categories may be treated in the same way (and thus by anatomically similar apparatuses). The following examples illustrate this statement:

— *Same food category but differing functional demands*: Cichlid eggs may be sucked from the substrate ("stolen" from a spawning couple: the egg-snatcher *Haplochromis barbarae* LV; WITTE-MAAS, 1981) or sucked from the mouth of a brooding female (snout-engulfing paedophage like *H. "rostrodon"* LV; WILHELM, 1980). These two species differ conspicuously in the form of their feeding apparatus. Not unexpectedly that of *H. barbarae* resembles that of a benthic feeding insectivore like *H. elegans* LG (ANKER, 1978; BAREL *et al.*, 1976), whilst that of the snout-engulfing is morphologically closest to the feeding apparatus of piscivores. From a functional morphological interpretation of these anatomical comparisons plus the data on the stomach contents, the two different predatory techniques were predicted before they were ac-

tually observed (GREENWOOD, 1959 and BAREL *et al.*, 1976, 1977 for snout-engulfing; BAREL *et al.*, 1977 for egg-snatching).

That one food-category (especially as used by cichlid ecologists) could imply a diversity of functional demands is also strongly suggested by the intratrophic differentiation of the haplochromine piscivores from Lake Victoria (VAN OIJEN, 1982). The morphology of the feeding apparatuses of these 70+ predatory species is certainly not uniform. According to VAN OIJEN (*op. cit.*) each type of a piscivorous feeding apparatus correlates with a complex of functional demands to be derived from *e.g.*: (a) the type of fish eaten (*viz.* cichlids and /or cyprinids) *plus* (b) the size of the prey *plus* (c) the predatory act (ambush or pursuit hunting) *plus* (d) the combination of prey types (fish only or fish and insects in approximately equal quantities). Similar examples of 'food to function' analyses at the intratrophic level of functional morphology are available for molluscivorous cichlids (HOOGERHOUD, *in prep.*), and zooplanktivorous cichlids (WITTE, GOLDSCHMIDT and BAREL, *in prep.*).

— *Differing food categories but same functional demands*: For the oral jaws and expansion apparatus '*feeding on cichlid eggs*' is not an unequivocal functional demand: it should be further specified (sucking from a substrate or snout-engulfing). However, for the *pharyngeal* jaw apparatus (PJA) '*feeding on cichlid eggs*' means only the transport of small items into the esophagus without mechanical trituration by the PJA. The food-categories zooplankton, phytoplankton, fish scales, fish parasites, epilithic and epiphytic algae represent similar small items. To a certain extent the PJA's of haplochromines feeding on such items (including cichlid eggs) are morphologically similar: *e.g.*, small pharyngeal jaws with tiny teeth and little developed pharyngeal muscles (see p. 398 and fig. 31).

The relations between food-category and function is an essential problem when ecology and functional morphology are integrated: *e.g.* in the analyses of potential niche width and ecological morphology. This aspect is further considered below.

— *Differing food-categories and partly similar functional demands*: This aspect was discussed in the section on the definition of core functions (p. 361).

The Morphological Basis of (In)Compatibility of Functions

Introduction

Functions, even when executed by different anatomical structures (*i.e.* apparatuses), cannot be randomly combined: spatial constraints determine to a major extent what combinations of apparatuses (and

thus functions) can or cannot be accommodated in a certain space (*viz.* the head). This is the main conclusion from the present analysis of spatial relations between various apparatuses in the heads of lacustrine cichlids. The spatial constraints on function combinations often imply a certain degree of incompatibility between the functions and (only rarely) in extreme cases an exclusion. This statement is best exemplified by the studies on bipartite relations between apparatuses, but as will be discussed further on, most likely holds even more for tripartite and multiple relations.

Function relations derived from bipartite spatial relations

1) *Expansion apparatus (EA) and pharyngeal jaw apparatus (PJA)*. In the series “*snout-engulfing paedophage*” → “*ambush huntig piscivore*” → “*pharyngeal crushing molluscivore*” the increase in the size (and thus probably in the power) of the PJA correlates with a decrease in the size (and thus probably the power) of the expansion muscles. The resulting trophic limitations are selfevident. Neither paedophages nor mollusc-crushers can lacerate larger fishes with their PJA. Paedophages should be able to feed on small preys; indeed at least some of them feed on zooplankton (WANDERA, *pers. comm.*).

2) *The oral jaw apparatus (OJA) and expansion apparatus (EA)*. Decreased lower jaw lengths, reduced protrusibility of the premaxillae, increased inclination of the dentigerous area and increased cross-section of the m. adductor mandibulae, all contribute to a greater biting force and a decrease in the volume and expansion-efficiency of the buccal cavity (p. 377). This implies that for a certain neurocranial length the specimen with the greater biting force needs more energy to suck a prey, and that the maximum size of a sucked prey can be necessarily smaller than the maximum prey of a sucked prey of the specimen with less biting force. Realize that within the OJA-EA context there are for *suckers* no spatial constraints on the possession of an EA morphologically adapted to sucking smaller prey only. The maximally expanded buccal cavities of zooplanktivores among the Lake Victoria haplochromines are smaller (less deep) than those of piscivores with the same neurocranial length (and the same body shape). Morphologically this smaller size of the buccal cavities of non-straining zooplanktivores is related to differences in the size of the hyoid (figs. 13, 34), and the sizes (fig. 4) and forms of the lower jaws.

Whether cichlids with rotationally asymmetric, expanded cavities (*e.g.* extreme biters and pharyngeal mollusc-crushers) would still be reasonably acceptable suction-feeders, cannot be predicted from the hydrodynamic models (made by Osse, Muller and van Leeuwen) which require rotational symmetry. However, indications for the inef-

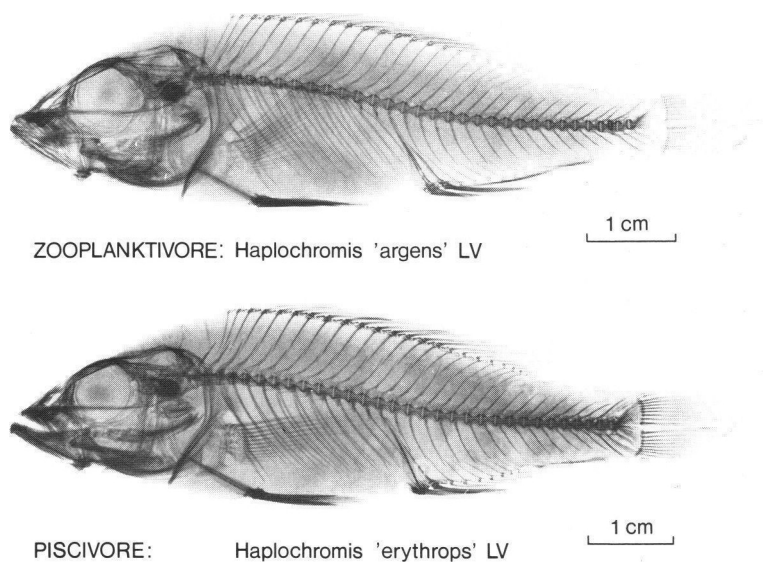


Fig. 34. Radiographs illustrating structural differences in the heads of two sucker species with similar body shapes. Note the shorter hyoids and smaller pharyngeal jaws in the zooplanktivore. The same observations have been made for comparisons between other piscivorous and (non-straining) zooplanktivorous species of various lakes.

iciency (or incapability) of such asymmetric cavities stems from stomach content analysis of species studied over various seasons. In the oral shelling molluscivore *Haplochromis sauvagei* LV zooplankton is a negligible item (KATUNZI, 1983). In pharyngeal mollusc-crushers like *H. ptistes* LV, *H. tegeelaari* LV, *H. mylergates* LV zooplankton was virtually never observed (HOGERHOUD, *pers. comm.*). For the oral shelling (crushing?) molluscivore *Chilotilapia rhoadesi* LM only soft remains of gastropods are mentioned as stomach contents (RIBBINK *et al.*, 1983). (But in this case I do not know over what period the observations were made.) Further hydrodynamic studies on extreme biters in combination with constructional morphology and prolonged ecological observations are required to test the hypothesis that, with increasing biting capacity, the suction capacity decreases (or even becomes excluded).

3) *Oral jaw apparatus and gill apparatus.* In the transformation from sucker to biter, the mediad expanding mAM forces the ceratobranchial to take a more oblique position which means more space for the gill lamellae. This positive correlation between the size of two apparatuses could also mean a positive correlation between the biting force and certain gill-functions (*e.g.* oxygen extraction capacity).

Function relations derived from tripartite spatial relations

Increase in streamline decreases the space for the epaxial and hypaxial muscles (the main operators of head expansion, p. 380). However, *this* inverse spatial relation probably does not imply an inverse relation between swimming speed and suction-capacity (but see below): active head expansion (resulting from contraction of the expansion muscles) and swimming speed are complementary mechanisms making water stream into the buccal cavity. For suckers I have no indications that the maximum buccal volume is influenced by increased streamlining. However, in biters, an *increased* head-depth (fig. 14) is necessary to maintain a radius of the buccal cone similar to that in suckers of the same neurocranial length. Streamlining has the reverse effect as is evident from the slender-bodied lepidophage *Perissodus paradoxus* LT, which has an extremely short sagittal distance between the hyoid-suspensorium articulation and the parasphenoid (fig. 14: arrow). This, its extremely short hyoid (fig. 13: arrow) (related to its greatly developed biting oral jaw apparatus) and other anatomical features suggest a highly reduced buccal volume. The species lives in the water column (*i.e.* not benthic) of fairly shallow water and feeds on scales (POLL, 1956). Anatomically one gains the impression that *Perissodus paradoxus* is a fast-swimming biter (a combination not often seen in cichlids). The *anatomical* evidence for its capacity to swim fast are its extremely long body (see below) and its frequency of secondary lamellae (32/mm; GALIS, *pers. comm.*). This frequency is high for a fish of this size (SL 173 mm) not living in oxygen-poor water and corresponds with the frequency of other fast swimmers (*cf.* GALIS & BAREL, 1980). The interpretation is corroborated by a comparison with *Perissodus hecqui* LT, a deeper bodied benthic lepidophage (also taking zooplankton; POLL, 1956; LIEM & STEWART, 1976) of which a specimen of 121 mm SL has 25.5 lamellae/mm (GALIS, *pers. comm.*).

The wide and obtuse head of *P. paradoxus* seems to be a drawback for fast swimming, but is possibly compensated for by the body which is long compared with that of fast swimming suckers (fig. 35). Obtuse lateral profiles are an advantage when acceleration plus turning are required (p. 383). The shallow body depth plus the obtuse lateral profile could be an optimal constructional compromise when fast swimming plus turning and acceleration are required. Such locomotory capacities could well be requirements of a scale eating fish "grazing" from an elusive prey.

From the foregoing suppositions arises a picture of a complex tripartite balance between the functions *swimming*, *suction feeding* and *biting*. It suggests that a fast swimming cichlid can either have a well-developed capacity for suction feeding, but then has a reduced biting

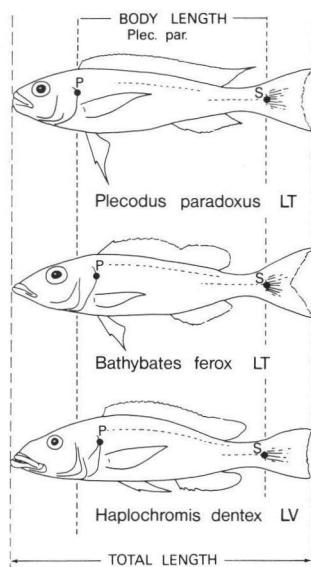


Fig. 35. Head length and body length of a slender-bodied biter, the lepidophage *Plecodus* (= *Perissodus*) *paradoxus* compared with slender-bodied suckers (*viz.* piscivores).

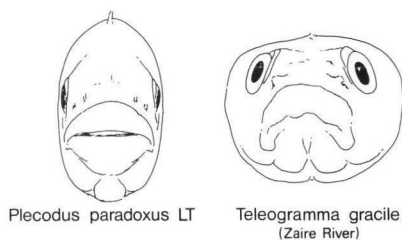


Fig. 36. Differences in head outlines of a lacustrine, slender-bodied biter (the lepidophage *Plecodus* [= *Perissodus*] *paradoxus*) and a slender-bodied, rheophilic biter (*T. gracilis* living in rapids).

force, or a powerful bite and then a highly reduced (virtually absent?) suction capacity. When moderate biting and suction are to be combined, fast swimming would be excluded (high neurocranial vault required, p. 380, which would not allow a slender body).

Elongated bodies with a rounded cross-section like that of *Perissodus paradoxus* LT are also characteristics of cichlids living in fast-flowing waters (ROBERTS & STEWART, 1976). However, whereas in relation to the required thrust from the body, the long axis of the (elliptically shaped) cross-section runs dorsad-ventrad in the fast swimming lacustrine biters, it runs mediad-laterad in the elliptically shaped

cross-section of the greater, rostral part of the body of *Teleogramma gracile* from the rapids of the Zaire River (fig. 36). The dorsad-ventrad compression of this fluviatile species allows a firm contact with the substrate (the well-developed pelvic fins and muscles serve for attachment to the substrate) and/or hiding below stones. In the head region this shape of the cross-section is correlated with a (virtually) absent supraoccipital crest (and a very shallow pharyngeal apophysis!; GREENWOOD, 1978) and with well-developed adductor mandibulae muscles which bulge laterad to the plane through the preoperculum. In lacustrine cichlids the lateral face of the adductor muscles is always flat and in the plane through the preoperculum (fig. 36). Possibly the well-developed biting oral jaw apparatus of this rheophilic cichlid is a compensation for a loss of suction capacity, which could both (loss + compensation) be constructional effects of the required cross-sectional outline.

Constructional Morphology and Ecology: Ecological Morphology

LIEM (1979, 1980) was the first to question the idea that cichlids with a conspicuous morphological adaptation to a certain food type are consequently restricted to this food type. His experiments demonstrated unequivocally that, for instance, the algae scraper *Petrotilapia tridentiger* LM, beside its expected feeding repertoire, at least in tanks, also performs various forms of suction feeding. Later field-observations corroborated the ecological value of these results: Many rock frequenting cichlids of Lake Malawi (including *Petrotilapia* spp.) do feed on zooplankton when it is abundant near the rocks (McKAY & MARSH*, 1983; RIBBINK *et al.*, 1983). Liem's *experimental* data on the unexpectedly large width of the feeding repertoire in tanks presented to him a "paradox ... that the morphologically and phylogenetically most specialized cichlid taxa are not only remarkable specialists but also "jacks-of-all-trades" (LIEM, 1981: 211, 212 and, with virtually the same words, 1980: 317). In fact, there is no question of a paradox as I shall try to demonstrate. In essence the same paradox is suggested by McKAYE & MARSH (*op. cit.*: 246) who after having demonstrated the

* McKAYE & MARSH (1983) give two references in which Liem's conclusions would have been criticized as being laboratory artefacts. One reference is "Liem, pers. comm.", the other is BAREL (1980). However, in my paper no such critical comment is made. A translation from the originally Dutch text of the section dealing with LIEM (1979, 1980) is given (BAREL, 1980: 232): "It is also important to know that the feeding movements of the ruff and the pike-perch are efficiently adjusted to the kind of prey (ELSHOUD-OLDENHAVE & OSSE, 1976; ELSHOUD-OLDENHAVE (1979). This idea has been further elaborated for chichlids by Liem who called it *modulatory multiplicity* (LIEM, 1979, 1980)".

ecological validity of Liem's aquarium-observations, raise the following question: "Can a population evolve to exploit one trophic resource more effectively and simultaneously broaden, or at least maintain, the ability to utilize a wide range of resources". However, phrased in this way, an inconsistent dilemma is created: if efficiency is the criterion for the exploitation of one resource, then efficiency (and not simply ability or inability) should also be the reference measure for the remaining resources. Liem and McKaye & Marsh focus on the most conspicuous adaptation (*viz.* the oral jaw apparatus of the algae scrapers). However, conspicuousness is not necessarily a relevant and/or the only criterion. Besides, the authors accentuate the trophic specialization for algae scraping but do not investigate two other questions essentially complementary to the recognized adaptation: what are the morphological requirements for feeding on the remaining ("facultative") food items and how can feeding on those items be combined morphologically with feeding on *e.g.* epilithic algae.

Before entering upon this problem a further remark on the possibly misleading connotation of "morphologically specialized". "Specialized" has the connotation of being adapted to perform a particular activity (and consequently being restricted in other activities). In algae scrapers, oral-crushing molluscivores, and in scale scrapers the conspicuous jaw structures are easily correlated with their diets. In zooplanktivores the adaptations for zooplankton-sucking (compared with the fish-sucking of piscivores) are less conspicuous but do exist in the shape of the lower jaw and the structure of the expansion apparatus. It is my experience that in cichlids functionally relevant anatomical differences are often fairly inconspicuous and are quantitative only. Nevertheless such small differences, like the frequency of the secondary gill lamellae, are apparently sufficient to keep species, which are otherwise ecologically similar, distributed over different habitats (GALIS & BAREL, 1980; HOOGERHOUD *et al.*, 1983).

The most extensive feeding repertoire observed by Liem and McKaye & Marsh was for species classified by me as biters. These repertoires require at least an executing of the two core functions, namely sucking and biting. As mentioned before these two core functions are to a certain extent compatible. At least biters with conically shaped oral cavities should be capable of suction-feeding. *Constructionally* the conical shape is due to spatial demands of the oral jaw apparatus (p. 375). *Functionally* such expanding profiles are dynamically more flexible in manipulating the waterflow than are cylindrical profiles (which are found in the piscivores) (MULLER & OSSE, 1983). This correlates well with the various types of suction-feeding distinguished by Liem in the feeding repertoire of the algae scraping biter

Petrotilapia, which indeed has a conically shaped oral cavity (pers. obs.). As shown algae scraping can be combined with sucking, but then, due to spatial and functional demands of the involved structures, sustained fast swimming and sucking of large items are excluded, and the costs of suction feeding are higher (p. 379) than in fishes with a well-developed protrusion. The exclusion of the functions “*sustained fast swimming*” and “*feeding on larger items*” leads to the question whether the species with the broader feeding repertoire deserve the title “jack-of-all-trades”. Even the cichlids with the broadest feeding repertoire take only a certain and relatively small section of all items exploited by cichlids as a whole. In that sense the qualification “all trades” is hyperbolic. In Lake Victoria those haplochromine species of which the food-preferences were studied over several seasons (and often over several years) all had a limited dietary range (VAN OIJEN, 1982; KATUNZI, 1983; WITTE, *in press*; HOOGERHOUD and GOLDSCHMIDT, *pers. comm.*) even those which would on morphological ground be classified as generalists (HOOGERHOUD *et al.*, 1983). This all suggests a specific limitation in food-selection under natural conditions. In combination with other observed ecological restrictions (*e.g.* limited depth range and substrate), I would conclude (also in a hyperbolic sense) that no cichlid is a “jack-of-all-trades” but that every cichlid is a “jack-of-a-few-trades”.

As treated by Liem and McKaye & Marsh the issue “trophic adaptation” is further underdetermined by not “translating” food-categories into functional demands. Once a fish has a well-developed suction capacity for small items, it is less relevant whether these items are zooplankton, small fishes or fish eggs. In other words, the number of food-categories is not a reference measure for the required morphology (see p. 404). Also for this reason Liem’s paradox is more apparent than real. One could argue that those functional capacities which allow most food-categories to be eaten are the best contribution to the animal’s fitness and thus to its evolutionary success. However, fitness cannot be measured from *trophic* versatility alone! First the energy costs are to be taken into account (zooplankton eating can be combined with feeding on epilithic algae, but my results suggest that the costs of eating zooplankton with a protrusile apparatus -which exclude algae scraping- are lower). Second the relation with non-trophic functions should not be overlooked. Efficient suction feeding may exclude food-items requiring biting. It does, however, allow a slender body for efficient fast swimming, which in this way could contribute to the animal’s overall fitness (hunting for fast prey, increasing its action radius, increasing its chances of escape from a predator). It is the overall functional repertoire and resulting ecological potentials that

should be considered when models for evolution are attempted. Hopefully, constructional morphology can be instrumental in such efforts.

To a certain extent I endorse the warning by McKAYE & MARSH (1983: 248) "...that it may be unwarranted to extrapolate from morphological specializations in apparatus to an animal's general diet or food preferences". As outlined above, one should not restrict oneself to the conspicuous specializations, but even when "*morphological specialization in*" is replaced by "*morphology*", neither constructional morphology, nor aquarium-observations can predict what actual range of food items an animal can take under natural conditions. In the complex relation between anatomical structure and the ecology of a species constructional morphology is an interphase with which one may predict what functions are compatible and what conditions there are for their compatibility (*e.g.* decrease in efficiency). This insight in function compatibility in combination with the data* from the natural environment* (and with aquarium observations) can then be used to predict deductively what the potential niche of the species is. An important complement and test for the deductive procedure for niche-predictions is the possibility of indicating what resources in the environment can *not* be used. Whereas the non-exploitation of a potentially allowed resource could be explained by *e.g.* competition, the exploitation of an unallowed resource would mean a falsification of the hypothesis.

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* *i.e.* data *not* including the investigated fish.

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APPENDIX

Abbreviations

| | |
|-----|-------------------------------------|
| Aw | Width of the m. adductor mandibulae |
| Ad | Depth of the m. adductor mandibulae |
| BM | Barombi Mbo |
| CC | Cuatro Cienegas Basin (Mexico) |
| EA | Expansion Apparatus |
| LG | Lake George |
| LM | Lake Malawi |
| LT | Lake Tanganyika |
| LV | Lake Victoria |
| mAM | m. adductor mandibulae |

| | |
|-----|--------------------------|
| NL | Neurocranial length |
| OJA | Oral jaw apparatus |
| OHS | Outer head shape |
| PJA | Pharyngeal jaw apparatus |
| SL | Standard length |
| ZR | Zaire River |

Following the convention of BAREL *et al.*, 1976 the ending -ad of of topographical adjective is used when a direction is meant and -al when a position is concerned.

TABLE I

List of specimens studied and their basic data. Names in quotation-marks concern as yet undescribed species of which reference collections are present in the Rijksmuseum van Natuurlijke Historie (Leiden)

| Species | Origin ¹ | Specimen | NL ² (mm) | JL ³ (mm) | Symbol ⁴ | Food ⁵ | Collection ⁶ /collector |
|---|---------------------|-----------|-------------------------|-------------------------|---------------------|-------------------|------------------------------------|
| <i>angusticeps</i> , <i>Serranochromis</i> | — | W.201.001 | 48.5 | 34.3 | △ | fish | 1932.12.16: 523-530 |
| "argens", <i>Haplochromis</i> | LV | W.239.004 | 17.0 | 9.5 | □ | zooplankton | HEST |
| "argens", <i>Haplochromis</i> | LV | W.239.006 | — | 9.2 | □ | zooplankton | HEST |
| <i>argenteus</i> , <i>Haplochromis</i> ^{7a} | LV | W.045.004 | — | 28.9 | △ | fish | HEST |
| <i>babaulti</i> , <i>Simochromis</i> | LT | W.144.001 | 16.3 | 7.1 | ■ | algae? | 1960.9.30: 1313-1317 |
| <i>barbarae</i> , <i>Haplochromis</i> ^{7b} | LV | W.043.001 | — | 11.4 | ○ | eggs | 1966.3.9: 244-251 |
| <i>bicolor</i> , <i>Macropocheurodus</i> | LV | W.036.001 | 25.0 | 10.9 | + | molluscs | 1955.2.10: 65-73 |
| <i>bicolor</i> , <i>Macropocheurodus</i> | LV | W.036.007 | 25.3 | 12.0 | + | molluscs | HEST |
| <i>bicolor</i> , <i>Macropocheurodus</i> | LV | W.036.008 | 23.3 | 11.5 | + | molluscs | HEST |
| <i>bicolor</i> , <i>Macropocheurodus</i> | LV | W.036.010 | 28.6 | — | + | molluscs | HEST |
| <i>bicolor</i> , <i>Macropocheurodus</i> | LV | W.036.018 | 25.4 | — | + | molluscs | HEST |
| "big teeth", <i>Haplochromis</i> | LV | W.255.001 | 32.4 | 20.8 | △ | fish | HEST |
| "big teeth", <i>Haplochromis</i> | LV | W.255.003 | — | 21.9 | △ | fish | HEST |
| "black cryptodon", <i>Haplochromis</i> | LV | W.291.001 | 27.5 | — | ○ | larvae/eggs | HEST |
| "black cryptodon", <i>Haplochromis</i> | LV | W.291.003 | — | 13.9 | ○ | larvae/eggs | HEST |
| "chlorocephalus", <i>Haplochromis</i> | LV | W.311.001 | 19.7 | 10.5 | □ | zooplankton | HEST |
| "chlorocephalus", <i>Haplochromis</i> | LV | W.311.004 | 20.0 | 10.9 | □ | zooplankton | HEST |
| "chlorocephalus", <i>Haplochromis</i> | LM | W.129.001 | 26.7 | 13.2 | □ | zooplankton | 1935.6.14: 1833-1844 |
| <i>chrysonota</i> , <i>Cyrtocara</i> | LM | W.130.001 | 45.0 | 23.0 | △ | fish | 1935.6.14: 591-595 |
| <i>compressiceps</i> , <i>Cyrtocara</i> | LV | W.319.002 | 18.4 | 8.9 | □ | zooplankton | HEST |
| "coop", <i>Haplochromis</i> | LV | W.227.002 | 17.7 | — | □ | zooplankton | HEST |
| "crimson", <i>Haplochromis</i> | LV | W.206.085 | 23.4 | — | ⊗ | prawns? | Anker/Barel |
| <i>croceoplus</i> , <i>Haplochromis</i> ^{7a} | LV | W.044.011 | 25.3 | 14.6 | ○ | larvae/eggs | 1958.1.16: 37-62 |
| <i>cryptodon</i> , <i>Haplochromis</i> ^{7c} | LV | W.109.005 | — | 16.5 | ⊗ | prawns? | Anker/Barel |
| <i>cryptogramma</i> , <i>Haplochromis</i> ^{7a} | LV | W.109.011 | 25.7 | — | ⊗ | prawns? | Anker/Barel |

Table I (continued)

| Species | Origin ¹ | Specimen | NL ² (mm) | JL ³ (mm) | Symbol ⁴ | Food ⁵ | Collection ⁶ /collector |
|---|---------------------|-----------|-------------------------|-------------------------|---------------------|-------------------|------------------------------------|
| <i>cryptogramma</i> , <i>Haplochromis</i> ^{7a} | LV | W.109.012 | 23.8 | 14.5 | ☒ | prawns? | Anker/Barel |
| <i>curvifrons</i> , <i>Simochromis</i> | LT | W.142.001 | 21.1 | 8.1 | ■ | algae | 1955.4.12: 47-66 |
| <i>cyanostictus</i> , <i>Eretmodus</i> | LT | W.247.002 | 14.4 | 5.2 | ▲ | ? | 1950.4.1: 5171-5182 |
| <i>cyanostictus</i> , <i>Eretmodus</i> | LT | W.247.004 | 9.3 | — | ▲ | ? | K. Yamaoka |
| <i>degeni</i> , <i>Platytaeniodus</i> | LV | W.048.006 | 18.7 | 8.5 | + | molluscs? | HEST |
| <i>dentex</i> , <i>Haplochromis</i> ^{7a} | LV | W.074.007 | 32.7 | — | △ | fish | HEST |
| <i>diagramma</i> , <i>Simochromis</i> | LT | W.143.001 | 23.9 | 10.6 | ■ | algae? | 1950.4.1: 742-771 |
| <i>dichrouirus</i> , <i>Haplochromis</i> ^{7a} | LV | W.090.003 | 26.2 | — | △ | fish | Anker/Barel |
| <i>dichrouirus</i> , <i>Haplochromis</i> ^{7a} | LV | W.090.004 | 24.9 | 17.0 | △ | fish | Anker/Barel |
| <i>dichrouirus</i> , <i>Haplochromis</i> ^{7a} | LV | W.090.007 | 30.7 | — | △ | fish | HEST |
| “double stripe”, <i>Haplochromis</i> | LV | W.320.004 | 16.8 | 8.7 | □ | zooplankton | HEST |
| <i>duboisi</i> , <i>Tropheus</i> | LT | W.298.002 | — | 5.4 | ■ | algae? | KMMA 75-01-P-1-21 |
| <i>eduardianus</i> , <i>Haplochromis</i> ^{7b} | LG | W.017.015 | 16.5 | — | ● | scales? | Barel |
| <i>elegans</i> , <i>Pseudotropheus</i> | LM | W.285.002 | 25.3 | — | □ | algae? | D.S.C. Lewis |
| “erythro-cryptogramma”, <i>Haplochromis</i> | LV | W.289.002 | 22.1 | 12.5 | ☒ | prawns? | HEST |
| “erythro”, <i>Haplochromis</i> | LV | W.279.002 | — | 10.9 | △ | fish | HEST |
| “erythro”, <i>Haplochromis</i> | LV | W.279.005 | 22.0 | 12.5 | △ | fish | HEST |
| “erythro”, <i>Haplochromis</i> | LV | W.279.006 | — | 11.6 | △ | fish | HEST |
| <i>fasciatus</i> , <i>Petrochromis</i> | LT | W.165.001 | 19.7 | — | ■ | algae | 1950.4.1: 7614-7633 |
| <i>ferox</i> , <i>Bathybates</i> | LT | W.192.001 | 47.5 | — | △ | fish | 1950.4.1: 5325-5342 |
| <i>ferox</i> , <i>Rhamphochromis</i> | LM | W.170.001 | 44.5 | 25.2 | △ | fish | 1935.6.14: 2196-2199 |
| <i>fuellborni</i> , <i>Labeotropheus</i> | LM | W.170.002 | 55.5 | — | △ | fish | M. Stiassny |
| <i>fuellborni</i> , <i>Labeotropheus</i> | LM | W.167.001 | 25.7 | — | ■ | algae | 1965.10.26-8-13 |
| <i>fuellborni</i> , <i>Labeotropheus</i> | LM | W.167.004 | — | 6.7 | ■ | algae | D.S.C. Lewis |
| <i>fuellborni</i> , <i>Labeotropheus</i> | LM | W.167.005 | 19.5 | 7.8 | ■ | algae | D.S.C. Lewis |
| <i>fuscus</i> , <i>Pseudotropheus</i> | LM | W.119.001 | 19.1 | — | ■ | algae | 1965.10.25: 131-141 |
| <i>gilberti</i> , <i>Haplochromis</i> ^{7a} | LV | W.217.010 | 38.1 | — | △ | fish | HEST |

Table I (continued)

| Species | Origin ¹ | Specimen | NL ² (mm) | JL ³ (mm) | Symbol ⁴ | Food ⁵ | Collection ⁶ /collector |
|--|---------------------|-----------|-------------------------|-------------------------|---------------------|-------------------|------------------------------------|
| <i>gracile</i> , <i>Telegramma</i> | ZR | W.216.003 | — | — | — | — | 1976.5.21: 88-97 |
| <i>granti</i> , <i>Haplochromis</i> ^{7d} | LV | W.033.001 | 26.5 | 12.4 | + | molluscs | 1956.10.9: 160-163 |
| <i>granti</i> , <i>Haplochromis</i> ^{7d} | LV | W.033.007 | 22.3 | 10.5 | + | molluscs | HEST |
| <i>granti</i> , <i>Haplochromis</i> ^{7d} | LV | W.033.008 | 22.1 | — | + | molluscs | HEST |
| <i>graueri</i> , <i>Bathybates</i> | LT | W.163.001 | 44.2 | 24.9 | △ | fish | 1960.9.30: 6274-6283 |
| <i>graueri</i> , <i>Bathybates</i> | LT | W.163.003 | 35.5 | — | △ | fish | M. J. P. van Oijen |
| <i>heequi</i> , <i>Perissodus</i> | LT | W.178.001 | 29.0 | — | ● | scales | 1960.9.30: 6370-6373 |
| “heusinkveldi”, <i>Haplochromis</i> | LV | W.317.001 | 18.4 | 9.5 | □ | zooplankton | HEST |
| “heusinkveldi”, <i>Haplochromis</i> | LV | W.317.003 | — | 10.3 | □ | zooplankton | HEST |
| <i>irsacae</i> , <i>Tanganicodus</i> | LT | W.248.001 | — | 3.4 | ▲ | insects | 1971.2.19: 12-13 |
| <i>irsacae</i> , <i>Tanganicodus</i> | LT | W.248.005 | 10.1 | — | ▲ | insects | K. Yamaoka |
| <i>johnstoni</i> , <i>Docimodus</i> | LM | W.193.001 | 49.0 | 24.8 | ● | fins | 1936.6.14: 2054-2058 |
| <i>johnstoni</i> , <i>Docimodus</i> | LM | W.193.002 | 23.0 | 9.5 | ● | fins | D. S. C. Lewis |
| <i>johnstoni</i> , <i>Docimodus</i> | LM | W.193.004 | 18.8 | — | ● | fins | D. S. C. Lewis |
| <i>livingstonii</i> , <i>Cyrtocara</i> | LM | W.128.001 | 28.3 | 15.9 | △ | fish | 1935.6.14: 421-425 |
| <i>longiceps</i> , <i>Rhamphochromis</i> | LM | W.265.008 | 35.2 | — | △ | fish | M. Stiassny |
| <i>longirostris</i> , <i>Haplochromis</i> ^{7a} | LV | W.076.010 | 31.2 | — | △ | fish | Anker/Barel |
| <i>longirostris</i> , <i>Haplochromis</i> ^{7a} | LV | W.076.013 | — | 18.9 | △ | fish | HEST |
| <i>longirostris</i> , <i>Haplochromis</i> ^{7a} | LV | W.076.014 | 30.4 | 19.7 | △ | fish | HEST |
| <i>longirostris</i> , <i>Haplochromis</i> ^{7a} | LV | W.076.015 | 28.7 | — | △ | fish | HEST |
| <i>longirostris</i> , <i>Haplochromis</i> ^{7a} | BM | W.195.001 | 21.5 | 8.5 | ▲ | sponges | 1973.7.18: 117-136 |
| <i>maclareni</i> , <i>Pungu</i> | BM | W.195.003 | 16.3 | — | ▲ | sponges | 1973.7.18: 159-168 |
| <i>maclareni</i> , <i>Pungu</i> | LV | W.031.019 | — | 22.9 | △ | fish | Anker/Barel |
| <i>macrognaathus</i> , <i>Haplochromis</i> ^{7a} | LV | W.031.023 | 41.5 | — | △ | fish | Anker/Barel |
| <i>macrognaathus</i> , <i>Haplochromis</i> ^{7a} | LV | W.031.030 | 34.3 | — | △ | fish | HEST |
| <i>macrognaathus</i> , <i>Haplochromis</i> ^{7a} | LV | W.031.046 | 36.1 | — | △ | fish | HEST |
| <i>maculicauda</i> , <i>Labidochromis</i> | LM | W.286.002 | 12.7 | — | ▲ | insects | D. S. C. Lewis |
| <i>maculicauda</i> , <i>Labidochromis</i> | LM | W.286.003 | 13.3 | 4.9 | ▲ | insects | D. S. C. Lewis |

Table I (continued)

| Species | Origin ¹ | Specimen | NL ² (mm) | JL ³ (mm) | Symbol ⁴ | Food ⁵ | Collection ⁶ /collector |
|---|---------------------|-----------|-------------------------|-------------------------|---------------------|-------------------|------------------------------------|
| <i>maxillaris</i> , <i>Haplochromis</i> ^{7c} | LV | W.029.002 | — | 21.3 | ○ | larvae/eggs | 1958.16: 172-179 |
| “megalops-like”, <i>Haplochromis</i> | LV | W.321.001 | 18.1 | — | □ | zooplankton | HEST |
| <i>melanopterus</i> , <i>Haplochromis</i> ^{7c} | LV | W.056.002 | 24.7 | 13.5 | ○ | larvae/eggs | HEST |
| <i>melanopterus</i> , <i>Haplochromis</i> ^{7c} | LV | W.056.003 | 27.3 | — | ○ | larvae/eggs | HEST |
| <i>michaelti</i> , <i>Haplochromis</i> ^{7c} | LV | W.082.006 | 34.5 | — | △ | fish | Anker/Barel |
| <i>microdon</i> , <i>Haplochromis</i> ^{7c} | LV | W.037.001 | — | 18.6 | ○ | eggs/larvae | 1958.1.16: 25 |
| <i>microdon</i> , <i>Haplochromis</i> ^{7c} | LV | W.037.016 | — | 16.1 | ○ | eggs/larvae | Anker/Barel |
| <i>microdon</i> , <i>Haplochromis</i> ^{7c} | LV | W.037.018 | 22.3 | — | ○ | eggs/larvae | Anker/Barel |
| <i>microdon</i> , <i>Haplochromis</i> ^{7c} | LV | W.037.058 | 22.6 | 12.6 | ○ | eggs/larvae | Anker/Barel |
| <i>microlepis</i> , <i>Boulengerochromis</i> | LT | W.150.001 | 41.0 | 20.9 | △ | fish | Anker/Barel |
| <i>microlepis</i> , <i>Perissodus</i> | LT | W.148.001 | 15.4 | 5.9 | ● | scales | 1960.9.30: 2029-2082 |
| “micro-obesus”, <i>Haplochromis</i> | LV | W.238.002 | 18.8 | — | ○ | larvae/eggs | 1950.4.1: 1079-1090 |
| “micro-obesus”, <i>Haplochromis</i> | LV | W.238.003 | 17.9 | — | ○ | larvae/eggs | HEST |
| “micro-obesus”, <i>Haplochromis</i> | LV | W.238.004 | — | 9.5 | ○ | larvae/eggs | HEST |
| <i>minckleyi</i> , <i>Cichlasoma</i> | CC | W.342.001 | 29.9 | — | — | plants | I. Kornfield |
| <i>minckleyi</i> , <i>Cichlasoma</i> | CC | W.342.002 | 39.2 | — | — | snails | I. Kornfield |
| <i>minckleyi</i> , <i>Cichlasoma</i> | CC | W.342.003 | — | — | — | plants | I. Kornfield |
| <i>minckleyi</i> , <i>Cichlasoma</i> | CC | W.342.004 | — | — | — | snails | I. Kornfield |
| <i>mloto</i> , <i>Cyrtocara</i> | LM | W.282.002 | 25.4 | — | □ | zooplankton | D. S. C. Lewis |
| <i>mloto</i> , <i>Cyrtocara</i> | LM | W.282.004 | 27.4 | 11.9 | □ | zooplankton | D. S. C. Lewis |
| <i>mloto</i> , <i>Cyrtocara</i> | LM | W.282.005 | 27.4 | 12.3 | □ | zooplankton | D. S. C. Lewis |
| <i>moorii</i> , <i>Tropheus</i> | LT | W.140.001 | — | 8.0 | ■ | algae | 1950.4.1: 907-912 |
| <i>moorii</i> , <i>Tropheus</i> | LT | W.140.002 | 24.0 | 8.5 | ■ | algae | 1950.4.1: 907-912 |
| <i>moorii</i> , <i>Tropheus</i> | LT | W.140.003 | 16.3 | — | ■ | algae | KMMA 129259-326 |
| “Nafubo I. paed.”, <i>Haplochromis</i> | LV | W.314.001 | 23.0 | 12.7 | ○ | larvae/eggs | HEST |
| <i>nanoserranus</i> , <i>Haplochromis</i> ^{7a} | LV | W.212.001 | 22.9 | 13.7 | △ | fish | Anker/Barel |
| <i>nanoserranus</i> , <i>Haplochromis</i> ^{7a} | LV | W.212.008 | 21.0 | 12.6 | △ | fish | HEST |
| <i>nanoserranus</i> , <i>Haplochromis</i> ^{7a} | LV | W.212.013 | 26.7 | — | △ | fish | HEST |

Table I (continued)

| Species | Origin ¹ | Specimen | NL ² (mm) | JL ³ (mm) | Symbol ⁴ | Food ⁵ | Collection ⁶ /collector |
|--|---------------------|-----------|-------------------------|-------------------------|---------------------|-------------------|------------------------------------|
| <i>nigricans</i> , <i>Haplochromis</i> ^{7f} | LV | W.054.006 | 21.0 | — | ■ | algae | HEST |
| <i>nigricans</i> , <i>Haplochromis</i> ^{7f} | LV | W.054.009 | 20.0 | — | ■ | algae | HEST |
| <i>nigricans</i> , <i>Haplochromis</i> ^{7f} | LV | W.054.011 | 19.9 | 9.6 | ■ | algae | HEST |
| <i>nigricans</i> , <i>Haplochromis</i> ^{7f} | LV | W.054.016 | 19.7 | 9.1 | ■ | algae | HEST |
| <i>nigricans</i> , <i>Haplochromis</i> ^{7f} | LV | W.054.017 | 15.8 | 7.1 | ■ | algae | HEST |
| “n.l.j. obesus”, <i>Haplochromis</i> | LV | W.306.001 | 23.0 | — | ○ | larvae/eggs | HEST |
| “n.l.j. obesus”, <i>Haplochromis</i> | LV | W.306.002 | 25.2 | 15.4 | ○ | larvae/eggs | HEST |
| <i>obesus</i> , <i>Haplochromis</i> ^{7c} | LV | W.027.002 | 31.5 | 19.6 | ○ | larvae/eggs | BM(NH): unregistered |
| “orange head”, <i>Haplochromis</i> | LV | W.316.002 | 15.8 | 8.5 | □ | zooplankton | HEST |
| <i>pappenheimi</i> , <i>Haplochromis</i> ^{7g} | LG | W.010.007 | — | 8.9 | □ | zooplankton | Barel |
| <i>pappenheimi</i> , <i>Haplochromis</i> ^{7g} | LG | W.010.021 | 11.6 | — | □ | zooplankton | Barel |
| <i>paradoxus</i> , <i>Perissodus</i> | LT | W.149.001 | 31.5 | — | ● | scales | 1950.4.1: 5256-5275 |
| <i>paradoxus</i> , <i>Perissodus</i> | LT | W.149.002 | 30.1 | 12.3 | ● | scales | 1960.9.30: 5456-6467 |
| <i>parvidens</i> , <i>Haplochromis</i> ^{7c} | LV | W.032.001 | 38.2 | 25.4 | ○ | larvae/eggs | 1958.1.16: 116-129 |
| <i>parvidens</i> , <i>Haplochromis</i> ^{7c} | LV | W.032.009 | 25.4 | 17.0 | ○ | larvae/eggs | HEST |
| <i>percoides</i> , <i>Haplochromis</i> ^{7a} | LV | W.032.010 | 25.3 | — | ○ | larvae/eggs | HEST |
| <i>percoides</i> , <i>Haplochromis</i> ^{7a} | LV | W.080.006 | 21.1 | — | △ | fish | HEST |
| <i>permaxillaris</i> , <i>Limnochromis</i> | LT | W.080.008 | 22.9 | 14.5 | △ | fish | HEST |
| “piceatus-like”, <i>Haplochromis</i> | LV | W.160.001 | 28.3 | — | — | zooplankton | 1950.4.1: 1257-1261 |
| “piceatus-like”, <i>Haplochromis</i> | LV | W.237.003 | 15.4 | — | □ | zooplankton | HEST |
| “piceatus-like”, <i>Haplochromis</i> | LV | W.237.006 | 15.9 | 8.6 | □ | zooplankton | HEST |
| “piceatus-like”, <i>Haplochromis</i> | LV | W.237.007 | — | 7.9 | □ | zooplankton | HEST |
| “pink paedophage”, <i>Haplochromis</i> | LV | W.307.001 | 13.6 | — | ○ | larvae/eggs | HEST |
| <i>plagiostoma</i> , <i>Haplochromis</i> ^{7e} | LV | W.035.002 | 34.8 | 23.9 | △ | fish | 1962.3.2: 448 |
| <i>plagiostoma</i> , <i>Haplochromis</i> ^{7e} | LV | W.035.018 | 22.1 | — | △ | fish | HEST |
| <i>plagiostoma</i> , <i>Haplochromis</i> ^{7e} | LV | W.035.021 | 27.4 | — | △ | fish | HEST |
| <i>polyodon</i> , <i>Petrochromis</i> | LT | W.196.001 | 37.9 | — | ■ | algae | BM(NH): unregistered |
| <i>polyodon</i> , <i>Petrochromis</i> | LT | W.196.004 | 34.8 | 11.9 | ■ | algae | M. J. P. van Oijen |

Table I (continued)

| Species | Origin ¹ | Specimen | NL ² (mm) | JL ³ (mm) | Symbol ⁴ | Food ⁵ | Collection ⁶ /collector |
|---|---------------------|-----------|-------------------------|-------------------------|---------------------|-------------------|------------------------------------|
| <i>prodromus</i> , <i>Haplochromis</i> ⁸ | LV | W.020.001 | 27.0 | 11.5 | + | molluscs | 1956.10.9; 110-125 |
| <i>prodromus</i> , <i>Haplochromis</i> ⁸ | LV | W.020.004 | — | 14.6 | + | molluscs | Anker/Barel |
| <i>prodromus</i> , <i>Haplochromis</i> ⁸ | LV | W.020.009 | 23.6 | — | + | molluscs | Anker/Barel |
| <i>quadrinaculata</i> , <i>Cyrtocara</i> | LM | W.176.001 | 35.0 | 16.7 | □ | zooplankton | 1962.10.18; 119-128 |
| "reginus", <i>Haplochromis</i> | LV | W.310.002 | 18.0 | 8.4 | □ | zooplankton | HEST |
| "reginus", <i>Haplochromis</i> | LV | W.310.003 | — | 4.5 | □ | zooplankton | HEST |
| <i>retrodens</i> , <i>Hoplotilapia</i> | LV | W.049.012 | 29.7 | 15.7 | + | molluscs | Anker/Barel |
| <i>retrodens</i> , <i>Hoplotilapia</i> | LV | W.049.017 | 27.1 | — | + | molluscs | HEST |
| <i>rhoadesi</i> , <i>Chilotilapia</i> | LM | W.168.001 | 35.0 | 15.6 | + | molluscs | 1935.6.14; 2094-2100 |
| <i>rhoadesi</i> , <i>Chilotilapia</i> | LM | W.168.002 | 34.0 | — | + | molluscs | D. S. C. Lewis |
| <i>robustus</i> , <i>Serranochromis</i> | — | W.200.001 | 51.5 | 41.5 | + | fish | 1935.6.14; 2307-2316 |
| "rock-picker", <i>Haplochromis</i> | LV | W.226.001 | 21.1 | 7.6 | ▲ | insects | HEST |
| "rostridon", <i>Haplochromis</i> | LV | W.308.001 | 21.6 | 12.2 | ○ | larvae/eggs | HEST |
| <i>sauvagei</i> , <i>Haplochromis</i> ^{7d} | LV | W.022.011 | 20.9 | — | + | molluscs | HEST |
| <i>sauvagei</i> , <i>Haplochromis</i> ^{7d} | LV | W.022.016 | 22.3 | 8.3 | + | molluscs | HEST |
| "smoke", <i>Haplochromis</i> | LV | W.290.004 | 26.3 | 16.0 | △ | crabs | HEST |
| species, <i>Petrotilapia</i> | LM | W.284.003 | 27.8 | 11.8 | ■ | algae | D. S. C. Lewis |
| species, <i>Petrotilapia</i> | LM | W.284.004 | 27.6 | 13.4 | ■ | algae | D. S. C. Lewis |
| species, <i>Tropheus</i> | LT | W.282.001 | 20.7 | — | ■ | algae | M. J. P. van Oijen |
| <i>squamipinnis</i> , <i>Haplochromis</i> ^{7e} | LG | W.007.289 | 21.4 | — | △ | fish | Barel |
| <i>stenosoma</i> , <i>Hemibates</i> | LT | W.162.001 | 44.0 | 23.0 | △ | fish | 1961.11.22; 990-998 |
| <i>stenosoma</i> , <i>Hemibates</i> | LT | W.162.002 | 39.7 | 23.0 | △ | fish | M. J. P. van Oijen |
| <i>sulphureus</i> , <i>Haplochromis</i> ^{7a} | LV | W.210.001 | 23.9 | 14.0 | ⊠ | prawns? | 1977.1.10; 132-143 |
| "supramacrops", <i>Haplochromis</i> | LV | W.234.004 | 22.2 | 11.9 | □ | zooplankton | HEST |
| <i>taurinus</i> , <i>Haplochromis</i> | LG | W.004.009 | — | 12.0 | ○ | larvae/eggs? | Barel |
| <i>tetracanthus</i> , <i>Lamprologus</i> | LT | W.135.001 | 25.1 | — | △ | fish? | 1950.4.1; 6177-6202 |
| <i>tropheops</i> , <i>Pseudotropheus</i> | LM | W.120.001 | — | 7.4 | ■ | algae? | 1965.10.25; 68-85 |
| "velvet black", <i>Haplochromis</i> | LV | W.225.001 | 22.5 | 11.4 | ■ | algae | HEST |

Table I (continued)

| Species | Origin ¹ | Specimen | NL ² (mm) | JL ³ (mm) | Symbol ⁴ | Food ⁵ | Collection ⁶ /collector |
|--|---------------------|-----------|-------------------------|-------------------------|---------------------|-------------------|------------------------------------|
| <i>victorinus</i> , <i>Haplochromis</i> ^{7e} | LV | W.034.002 | 34.7 | 21.9 | △ | fish | 1962.3.2: 488-494 |
| <i>victorinus</i> , <i>Haplochromis</i> ^{7e} | LV | W.034.003 | 33.7 | — | △ | fish | 1962.3.2: 488-494 |
| "wh.l. obesus", <i>Haplochromis</i> | LV | W.305.002 | 21.0 | 12.7 | ○ | larvae/eggs | HEST |
| "wh.l. obesus", <i>Haplochromis</i> | LV | W.305.003 | 22.0 | — | ○ | larvae/eggs | HEST |
| <i>xenognathus</i> , <i>Haplochromis</i> ^{7d} | LV | W.023.007 | 22.1 | — | + | molluscs | HEST |
| <i>zebra</i> , <i>Pseudotropheus</i> | LM | W.118.002 | 19.0 | 10.0 | ■ | algae | D. S. C. Lewis |
| <i>zebra</i> , <i>Pseudotropheus</i> | LM | W.118.004 | — | 8.5 | ■ | algae | D. S. C. Lewis |

1. See appendix.
2. NL = neurocranial length, as defined by HOOGHERHOUD & WITTE, 1981. See inset in figures.
3. JL = length of the lower jaw. Virtually always this was measured between the centroid of the suspensorial articulation-facet and the rostral-dorsal corner of the symphysis (AD in fig. 1). Unfortunately in some cases the taxonomic lower jaw length (L_{JL} of BAREL *et al.*, 1977) was taken, but this never concerned specimens used in the published graphs with lower jaw length along one of the axes.
4. As used in the graphs.
5. A rough indication of the (or a) major food-item.
6. The long numbers concern specimens from the collections of the British Museum (Natural History), London. KMMA = Koninklijk Museum voor Midden Afrika, Tervuren, Belgium.
7. According to GREENWOOD (1980) this species should be placed in the genus: 7a *Prognathochromis*, 7b *Astatotilapia*, 7c *Lipochromis*, 7d *Pyochromis*, 7e *Harpagochromis*, 7f *Neochromis*, 7g *Yssichromis*.
8. According to GREENWOOD (1980) this species should be called *Pyochromis annexens*.